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No. 60

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OF THE

GOVERNMENT OF INDIA

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No. 4

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BY

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Studies on the Mouth Parts and Sucking Apparatus of the Blood-Sucking Diptera.

No. 4.

The Comparative Anatomy of the Proboscis in the Blood-Sucking Muscidæ.

IN two previous studies I have described the structure and mechanism of the proboscis in *Philæmatomyia insignis*, Austen, and *Lyperosia minuta*, Bezzi, and in doing so adhered as far as possible to the terms already in use for the various parts of the Muscid proboscis, thereby committing myself to the view that a close homology exists between them. So far as the gross anatomical features, such as the division of the proboscis into the three parts found in *Musca*, and the general shape and relations of the labrum-epipharynx and hypopharynx, are concerned, the homology is evident at a glance, but those structures which are immediately concerned in the act of biting, in accordance with the descriptions of the mechanism given in the papers mentioned above, are modified in remarkable manner, and to so great an extent that the relationship between them and the parts designated by the same name in *Musca* can only be properly understood when the intermediate forms are examined. In the present paper I propose to discuss the changes which have been produced in the Muscid type of proboscis in correlation with the adoption of a blood-sucking habit, and to show that the blood-sucking flies of this group can be arranged in a series, commencing with those flies which are blood-suckers by habit but have no biting mouth parts, and passing on through those flies which, while still retaining the *Musca* facies, are provided with more or less efficient biting organs, to those forms, such as *Stomoxys* and *Glossina*, which are typically blood-suckers, and have entirely lost the characteristic structure on the labella by means of which the non-biting flies absorb nourishment. Arranged in this manner those flies which I have been able to study form a most interesting series, in which the gradual progress of a change in structure along a definite path, correlated to a change in the habit of life, can be traced step by step from its origin to a stage in which the structural modification is extreme. The pointed and rigid proboscis of *Glossina*, typically a piercing organ, bears little or no superficial resemblance to the blunt and retractile organ of *Musca*, and yet there are few structures in the one which cannot be traced in the other, and the mechanism by which food is obtained is closely related in the two cases.

The flies which I have examined are as follows:—Three species of the genus *Philæmatomyia*, viz. *lineata*, Brunetti, *insignis*, Austen, and *gurnei*, Patton and Cragg; *Hæmatobia** *irritans*, Linn. *Stomoxys calcitrans*, Linn., *Lyperosia minuta*, Bezzi, and *exigua* Meij; *Glossina palpalis*, R. D., and *submorsitans*, Newstead. The order in which they are placed in the above list represents approximately the degree of specialisation which is found in their mouth parts, and this corresponds very closely with the positions assigned to the various genera by systematic dipterologists. The genus *Philæmatomyia* closely resembles the genus *Musca*, being distinguished from it mainly by the presence of a ring of biting teeth, the degree of development of which differs considerably in the three species so far known. *Hæmatobia* is remarkable in that, although the general shape and structure of the proboscis shows little difference from that of *Stomoxys*, traces of a pseudotracheal membrane still persist. The genus *Glossina* is placed by Austen in association with *Stomoxys* and *Lyperosia*; the condition of the mouth parts shows that it is more highly specialised than either, and the method of reproduction supports this view. *Stomoxys* and *Lyperosia* closely resemble one another, and the structure of the proboscis indicates that these flies have entirely abandoned food other than blood.

Before going further it will be well to discuss the general aspects of the question and to substantiate the hypothesis indicated in the opening paragraph, that the blood-sucking Muscids are derived from non-biting forms. Special attention is due to this point, for certain workers, notably Minchin and Prowasek, have assumed the contrary to be the case, and the former author has used this assumption as a support for the theory that the Hæmoflagellates are the descendants of organisms which originally inhabited the intestinal tract of vertebrates, and that the flagellates found so commonly in the digestive tract of insects are derived from Hæmoflagellates, those insects in which they occur being either blood-suckers or the descendants of blood-suckers. It would be out of place to discuss the purely parasitological aspect of this question here, but the subject is of sufficient importance to necessitate a consideration of the evidence there is in favour of or against the hypothesis from the entomological point of view.

In the first place, it must be remembered that the Diptera are simply a highly specialised division of the class Insecta, that the Insecta are Arthropods, and that the sucking mouth which is one of the main characteristics of the Diptera is a modification of a biting mouth. The remote ancestors of all Diptera were undoubtedly biting creatures, either animal or vegetable feeders, or predaceous. Even in the Diptera the sucking mouth shows varying degrees of development, and it is most improbable that there are any instances of

* And an undetermined Indian species.

reversion from the advanced condition to the earlier one. As I have shown in a previous paper, the biting flies in the Orthorrapha have a relatively simple form of apparatus, in which the primitive arthropod structures can be easily traced, for piercing the skin of the host. The sucking portion of the mouth is in fact formed by the simple apposition of the epipharynx and hypopharynx, while the true segmental appendages retain a form not at all unlike that found in quite primitive arthropods. *Tabanus*, for example, is a true " biting " insect, in the sense that it makes a wound by means of its mandibles and first maxillæ; the wound having been made, it sucks up the blood by means of a sucking pump in the head, through the canal formed by the apposition of the epipharynx and the hypopharynx, exactly as is done by non-biting flies which feed on vegetable or animal juices. The flies which possess functional mandibles and maxillæ are undoubtedly nearer the primitive arthropod type than those which have neither, and it is reasonable to suppose that, among the Orthorraphic flies, such forms as *Tabanus* are more primitive than the flower feeders, and that in those cases in which the female has a complete biting and sucking mouth and the male only a sucking mouth, the female is the less removed from the immediate ancestor of the species. The loss of the appendages, in this case, is an indication of specialisation. The mandibles and first maxillæ of the biting flies of this group are clearly primitive structures retained, and their existence is good evidence that the flies are more ancient than those which have lost them, due regard being given of course to other characters. In this case and in this limited sense the hypothesis of Minchin is supported by entomological considerations, and it is quite possible that the flagellates present in non-biting Orthorraphic flies have for their immediate ancestors similar parasites which inhabited the intestinal tract of blood-sucking flies.

The case is quite different with regard to the Cyclorraphic flies. In no case do these possess mandibles or first maxillæ, the only recognisable remnant of these being the palpi, which are believed to be remainders of the first maxillæ. The biting apparatus is developed on the labella, which are derived from the second maxillæ, appendages which take no part in the act of biting in the Orthorraphic flies. Not only is the apparatus formed out of different appendages, but it is of a different nature, and consists, as I have shown in the case of *Philæmatomyia* and *Lyperosia*, of an arrangement of teeth which are drawn through the wound by means of muscles situated in the labium. As will be shown in the course of this paper, these teeth are represented in the non-blood-sucking Muscids, and their development is the key to all the modifications found in the different forms.

The labella, at the end of the fused second maxillæ, are modified in most of the Diptera which do not suck blood into an apparatus of the nature of an absor-

bent pad, for the collection of fluid nourishment, which is sucked up the canal in the proboscis by means of the pharyngeal pump. The commonest form of this is the well known pseudotracheal membrane found in the house fly. This form of apparatus is not peculiar to the Muscid flies, but occurs in the Orthorraphic flies as well, and is absent only in those forms which obtain their nourishment by actually piercing some resistant layer to obtain fluid from underneath, and it is evident that its development is generally coincident with the disappearance of the biting appendages. In some instances, as for example the Tabanidæ, it exists side by side with functional and powerful mandibles and maxillæ, the fly being then able to absorb fluid either from a moist surface or through a resistant dry layer which has to be pierced by the stylets. In no case, however, does one find any form of biting apparatus on the labella existing together with functional mandibles or first maxillæ. The development of labellar teeth is a secondary phenomenon, which takes place when a non-biting fly, the mouth of which is adapted only for sucking fluids from moist surfaces, assumes the blood-sucking habit. How this occurs in nature will be discussed in more detail when dealing with those flies which are blood-suckers but are without biting mouth parts.

We may sum up the evolutionary history of the blood-sucking Diptera as follows. The early insect mouth parts were formed for biting and furnished with simple arthropod jaws: the cockroach represents such a condition. At a remote period the second pair of maxillæ became fused, a condition found in all Diptera. The sucking mouth characteristic of the Diptera is formed by the elongation of the epipharynx and hypopharynx, which together form a tube up which the fluid nourishment is sucked. In the most primitive dipterous types the typical arthropod appendages are retained, co-existent with the sucking tube, and the insect is able to use its appendages to pierce a hole in skin or other substance to obtain fluid food from underneath. Such a condition is found in the Orthorraphic blood-sucking flies. At a later period the appendages of the fourth and the fifth segments of the head, that is, the mandibles and maxillæ, disappear, and the function of obtaining food is carried out by the second maxillæ, the distal ends of which are modified to form a pad suitable for the absorption of fluid from moist surfaces. This condition is found in many families, both in the Orthorrapha and the Cyclorrapha. It reaches its highest degree of development in the complex labella of *Musca*. Still more recently some flies have developed from this stage a most complex arrangement consisting of a ring of teeth on the end of the labium, and have adapted themselves to a blood-sucking habit. Throughout the evolution there is to be noticed a constant diminution in the importance of the anterior appendages, and the gradual transfer-

ence of the entire function of obtaining food to the second maxillæ. These act in the more primitive forms merely as a sheath for the stylets, in the next stage as an absorbent pad, and in the last stage, that of the blood-sucking muscids, as cutting organs.

To return for a moment to the hypothesis of Minchin. All Diptera, and one may add all Hemiptera also, are descended from biting or mandibulate ancestors, but these ancestors were not necessarily blood-suckers, and consequently flagellates found in non-blood-sucking flies may or may not be descended from ancestors which were at one time hæmoflagellates. It is not to be supposed that there has been any direct line of descent, and it appears to me to be impossible to decide, in the present stage of our knowledge at least, whether those forms, which in the past gave rise to the non-blood-sucking flies we know to-day, were blood-suckers or not. Certainly they were provided with mouth parts which could be adapted for the purpose with comparatively little change, but there is no evidence of any importance one way or the other.

In the case of the Muscid biting flies Minchin's hypothesis can only be accepted in a limited sense. Enough has been said already to show that in this group the evolution has progressed from non-blood-sucker to blood-sucker and that the flies of the *Stomoxys* group are more recent than the simple *Musca* forms. That being the case, if the flagellates found in Muscid flies are descended from hæmoflagellates, then they can only have reached the fly at the remote period when the fly was mandibulate, before the appendages had atrophied from disuse. To be precise, if the ancestral stock of *Herpetomonas muscæ-domesticæ* at any time inhabited the blood of a vertebrate, it must have changed its habitat at that period in the evolution of the house fly when the mandibles and maxillæ were present and functional, and after the outgrowth of the labrum-epipharynx and hypopharynx had taken place; and this change can only have occurred if one of the mandibulate ancestors of *Musca domestica* happened to be also a blood-sucker. Before the formation of the sucking tube the insect was purely a biter, and probably lived on solid or semi-solid food, and after the disappearance of the mandibles and maxillæ it was purely a sucker, and could not make the necessary wound.

The statement made above, that the Muscid biting flies have for their immediate ancestors non-biting flies of the *Musca* type, is entirely in accord with the other features of their structure and life history. A detailed exposition of the reasons for the systematic position of the blood-sucking genera would be out of place here, but two points of importance may be noted in passing. In the first place, the venation of the wing shows characteristic changes. According

Note.—I have been unable to consult the paper quoted by Prowasek.—Fr. Brauer, Uber die Verbindungsglieder Zwichen den orthorrhaphen und cyclorrhaphen Dipteren, etc.—Verhandl. der zool-bot Gesellschaft, 1890, s. 273.

to no less an authority than Williston, a concentration of the wing veins towards the anterior margin, and a shortening of the most anterior veins, are evidence of specialisation, and once these changes have taken place they are irreversible ; a comparison of the venation of *Musca* and *Glossina* indicates clearly that the latter fly, according to this criterion, is the more recent of the two forms. Secondly, we find that a tendency towards the pupiparous habit, undoubtedly a recent development in the Diptera, and one which indicates a high degree of specialisation, appears along with the blood-sucking habit, though it occurs somewhat irregularly in the group. *Philæmatomyia insignis* is oviparous, but the eggs hatch in a remarkably short time and are larger when laid than one would expect for the size of the fly. *Stomoxys* and *Lyperosia* are normal in their reproduction ; *Glossina* approaches very closely to the Pupipara. As the Pupipara are typically blood-sucking and parasitic, there is evidently some relation between the method of obtaining nourishment and the method of reproduction. What this relation may be is not decided, but the modification of the reproductive organs and the divergence from the type found in other Diptera are so extreme that the descent of non-blood-sucking oviparous forms from blood-sucking pupiparous ones is not conceivable. The case is not comparable with the larviparous habit among the *Tachinidæ*, for the larvæ of many Muscid biting flies live in dung or other situations side by side with those of other oviparous Muscids, whereas those of Tachinids are usually deposited in the bodies of other larvæ, and a shortening of the immature stages is almost essential to the continuation of the race.

Without going into any further detail in this matter it will suffice to repeat that the arrangement of the Muscid biting flies in the above order, as more recent and more specialised than those Muscids which have mouth parts adapted only for the absorption of fluid from moist surfaces, is in agreement with the accepted systems of classification, which are for the most part founded on other anatomical or biological features. The theory that the flagellates of insects are descended from hæmoflagellates finds little support from entomological facts; how they originally reached the intestinal tract of the insect it is not the purpose of this paper to discuss.*

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* Note.—If I may be permitted to make a suggestion here, the argument of the above paragraphs may be carried further. At that remote geological period when the waters covered the earth, the great majority of insects, and arthropods which were destined to become insects, must have been aquatic or semi-aquatic in their habits ; during this phase of their evolution free living flagellates, presumably present in abundance then as now in water rich in organic matter, must have passed into the intestinal tract of the insect either as food or accidentally with the food. In the latter case, presuming that they were able to resist the action of the digestion by encystment in response to an unfavourable environment or otherwise, the conditions for the establishment of parasitism would be present, and the dependence of the flagellate on its insect host for the completion of its life cycle but a short step.

The Proboscis of Musca.

Since all the flies to be discussed in this paper are to be regarded as derived from a Musca-like ancestor, a brief note on the structure of the proboscis of this type must be given. Descriptions of the proboscis of *Musca* and the allied forms are numerous enough, and I have indeed little to add to what has already been said, but it will be necessary, in view of what follows, to define clearly what is meant by certain of the terms employed, and in certain cases to introduce new ones. Any points which I omit, and regarding which the reader may wish to refresh his memory, are dealt with in Kraepelin's complete account. The species which I have specially studied, and to which the description mainly applies, is *Musca nebulo*, the common bazaar fly of Madras. The differences between different species are however so small that the description will apply in all the important points to any species of like habit.

The proboscis of *Musca* consists of three parts, termed from above downwards the *rostrum*, *haustellum*, and the *labella*. Between each two of these, and between the rostrum and the head, there is a joint which permits of movement in a vertical plane. When the proboscis is in use, the three joints are extended so that the three parts are in the same straight line, and the whole proboscis hangs downwards from the under surface of the head of the fly, approximately at a right angle to the long axis of the body. When the proboscis is not in use it is retracted by the flexion of all three joints, in such a way that the three parts are folded on one another and tucked into an orifice on the under surface of the head. This orifice is termed by some systematists the "buccal orifice," an unfortunate name, for it is separated from the true mouth of the fly by the whole length of the pharynx, and is moreover merely an interval in the chitinous integument of the head, and has nothing to do with the buccal cavity. I propose to adopt the term *epistomal orifice* for this aperture. Of the three divisions enumerated above, the rostrum is, strictly speaking, a portion of the head. It contains the pharynx, and the only portion of the true mouth parts in relation to it is the pair of maxillary palps, which are attached to its anterior surface; the haustellum is the proboscis proper, and consists of the surviving head appendages, *viz.*, the second maxillæ, fused to form the labium, and the labrum-epipharynx and hypopharynx. The labella are parts of the second maxillæ which have remained separate at the distal end. The nature of the joints and the range and nature of the movements of the proboscis will be discussed later, but it should be noted here that the extension of the rostrum is of the nature of an evagination of a part of the head capsule. The so-called "buccal orifice" is merely a thickened rim where the rigid chitin of the head capsule gives place to the soft and flexible wall of the rostrum.

The Rostrum.

The rostrum has the shape of a truncated cone, broad end uppermost. Its outer covering consists of a flexible membrane which is continuous at the epistomal orifice with the chitin of the head capsule. At the distal end it is attached to the wall of the haustellum. Within this membrane there is a somewhat complex chitinous structure termed the fulcrum, part of which forms the pharynx or sucking pump of the fly. This structure affords the necessary rigidity to this part of the proboscis, and gives attachments to the various muscles which act on the joint between the rostrum and the haustellum.

The *fulcrum* resembles, to use Kraepelin's admirable simile, a Spanish stirrup iron. It consists of a posterior plate, two lateral plates, and an anterior arch. The posterior plate is oblong, slightly concave forwards anteriorly, and narrower above than below. Its upper and lower borders are incurved, the lateral angles of the former being produced upwards into a pair of stout cornua, which are also intimately connected with the lateral plates. The lateral plates are roughly triangular, and are continuous by their longest sides with the posterior plate, projecting forward at right angles from it; their upper sides are deeply incurved. The anterior side, which is much longer than the upper one, is also incurved, but the contour is abruptly broken at the junction of the middle and lower thirds by the projection forwards of a sharp spur, the border being more concave below than above this point. The anterior arch is situated at about the same level as the cornua on the posterior plate, and passes between the upper anterior angles of the lateral plates; it is a thick ridged bar, which gives attachment to part of the dilator muscles of the pharynx, and is the part which is pressed against the clypeus when the rostrum is rotated in retraction. It lies in, and is continuous with, the membraneous anterior wall of the rostrum.

The *pharynx*, or sucking pump, of *Musca* resembles that of the Orthorraphic flies, consisting of two superimposed chitinous plates, which can be separated by dilator muscles. The posterior of these plates is the one described above as the posterior plate of the fulcrum; the anterior plate, which lies in close contact with it when the organ is not in use, is of similar shape and extent, but is much thinner, and is drawn away from the other by the action of the dilator muscles. It has a thick ridge of chitin running down its middle line, to which the muscle fibres are attached. The anterior plate, however, is not simply pulled away from the other so as to leave a crecentic interval between the two, but is bent forwards on each side as the muscles pull the median ridge forward, so that the resulting cavity tends to be tri-radiate, an arrangement which recalls that of the pharynx of the mosquito. The

fulcrum lies in the anterior part of the rostrum; behind it there is a comparatively large space, which in the extended position is occupied by two large cylindrical air sacs, which are of great importance in the mechanism of extension.

In the middle line between these there is the salivary duct, and on either side and behind there are numerous muscles, which act on the joints above and below. These will be dealt with more particularly later.

The fulcrum does not extend quite to the lower end of the rostrum, and communication between the food canal in the haustellum and the pharynx is established by means of the intervention of a small chamber resembling a miniature pharynx. This has been elaborately described by Kraepelin, who, however, did not give it a definite name. Lowne termed the chitin forming its wall the "hyoid sclerite." When describing the corresponding structure in *Lyperosia* I suggested the name *buccal cavity* as having the double advantage of indicating at once the position and the homology. The chamber consists, in *Musca*, of a small triangular piece of thin chitin, arranged with its long axis pointing towards the haustellum, and its broad base between the lower cornua of the fulcrum, so that it occupies the interval between the two divisions of the proboscis. The lateral angles are bent forward, and are connected with one another by means of a thin membrane, which is also attached to the anterior plate of the pharynx. The epipharynx and hypopharynx terminate in the region of this cavity in a manner which will presently be described.

The Haustellum.

The main bulk of the haustellum consists of the *labium*, or fused second maxillæ. The other parts are concealed in a groove on its anterior surface in the normal conditions of the parts.

The labium is roughly cylindrical in shape, thickest in the middle, and tapering a little at each end. Its wall consists of two pieces of chitin united by a loose membrane, which is attached to the lateral edges of each. Of these the posterior, termed the *mentum* (Plate II, figure 3) and homologous with the mentum of other insects, is much the largest; it has the shape of a shallow trough, with the concavity directed forwards, and is contracted at its lower end. It forms the posterior and lateral walls of the labium, and has thickened lateral borders. The arrangement of the parts at its lower end should be particularly noted, as they undergo important modifications in the blood-sucking Muscids. The thickened lateral borders converge towards the distal end, and become somewhat attenuated; the distal border, which is about one-third the length of the lateral sides, has in its middle portion a deep square-shaped incision, on the opposing sides of which there are two longitudinal rod-like

thickenings of the chitin, extending the whole length of the sides of the incision. Continuous with these there is on each side a second rod of the same length as the sides of the incision; these two rods pass downwards distal to the lower border of the labium, and diverge from one another. They have an important connection with the chitinous arch which supports the labella behind. If they are examined in thoroughly cleared preparations, it will be seen that although they are continuous with one another, there is a distinct thinning of the chitin at the level of the distal border of the mentum, which suggests that the proximal and distal portions of the rod are moveable on one another.

The other chitinous portion of the labium is very ill defined in *Musca*, and can only be recognised in slightly cleared preparations and in sections. It is a thin sheet of chitin, grooved to form a shallow trough, and situated immediately behind the hypopharynx, the upper part of which is fused with it. On each side of this groove there is a rod-like thickening, which extends from a point a little distal to the base of the hypopharnyx to the labella, to the anterior sclerite of which it is attached. The groove, with its lateral thickenings, may be termed the *labial gutter*. It corresponds to the structure described in *Stomoxys* under that name by Stephens and Newstead.

The membrane which unites the anterior and posterior plates of chitin, and completes the wall of the labium, is in *Musca* very lax and of considerable extent. The two chitinous portions are not continuous with one another at any point.

The chief contents of the labium are the muscles which move the labella; these will be briefly described in connection with the mechanism of the proboscis. In addition there is the labial salivary gland, situated behind the lower end of the labial gutter, and a nerve and trachea on each side. There are no air sacs in the labium and the tracheæ are little larger than the nerves.

The *labrum-epipharynx* (Plate II, figure 5) lies in the groove on the anterior surface of the labium. It is shaped like a lance-head, its greatest breadth being about one-third of its total length. There appears to be some difference of opinion with regard to the composition of this organ, and the terms labrum and labrum-epipharynx are used somewhat loosely in current literature. If one bears in mind that the organ in *Musca* is homologous with the one in the more primitive Orthorraphic flies its dual nature will be evident. The outer part of the organ consists of the labral element. It gives its shape to the structure, and, arching over the anterior and lateral sides, terminates at about the middle third of the posterior surface. The inner portion is the epipharynx, and consists of a gutter having a depth of about half a circle. Between these two chitinous parts there is an interval, which is partly occupied by a fan-shaped

muscle passing from the labrum to the epipharynx. The method of termination of the two constituent parts indicates clearly their different origin, for at the proximal end they separate completely. The broad upper end of the labrum becomes continuous with the membrane on the anterior surface of the rostrum, and this of course is directly continuous with the clypeus of the head capsule; the only real difference in the relations of the labrum in the Muscid flies is that it has become separated from the head by the evagination of the rostrum from the head cavity. At the sides of its upper border there are small pits for the articulation of the labral apodemes, stout and heavily pigmented rods which pass upwards and outwards, diverging from one another, into the rostrum. The lower ends of the apodemes are pointed and barbed, the main portion of the rod slightly sinuous, and the upper end expanded for muscle attachment. Some of the muscle fibres attached to these apodemes are probably representatives of the labral muscles found in the Orthorraphic flies, and the apodemes themselves may be derived from the portion of the labrum which in the more primitive group is to be found inside the head capsule, and to which the muscle of the labrum is attached. The upper end of the epipharynx is a considerable distance proximal to that of the labrum, for it projects into the rostrum as far as the upper part of the buccal cavity, to the upper border of which it is connected by means of a soft membrane. In view of the similarity in all essential points between the labrum-epipharynx in *Musca* and that in the Orthorraphic flies, in which the epipharynx is in direct chitinous continuity with the functional buccal cavity, I do not see any grounds for accepting Kraepelin's view, that the organ is a mere evagination from the head cavity.

The *hypopharynx* retains the structure usual in the Diptera, being a simple spatulate slip perforated by the salivary duct. Its proximal third is fused with the labial gutter. At its upper end it projects into the rostrum behind the epipharynx, and is attached by a fine membrane to the pointed end of the triangular plate which forms the main part of the buccal cavity. It will now be evident that the buccal cavity is completed in its distal portion by the attachment to it of the epipharynx and the hypopharynx, which converge together at this point, and are united to the borders of the chitinous plate by membrane. This point, therefore, as correctly stated by Kraepelin, is the true mouth of the fly. It will be shown later that as the blood-sucking proboscis is evolved, the mouth is moved forwards, and the buccal cavity transformed into a tube with complex walls.

I have already noted, in a previous paper, that the hypopharynx, like the labrum-epipharynx, consists of two distinct laminæ, which enclose between them the salivary duct. In *Musca* the labial lamina is only separate in the

distal third of the organ. Separation of whole of this lamina with the formation of a free organ is found in the flies to be discussed later. The *salivary duct* emerges from between the two laminæ just above the point of union of the stomadael element with the walls of the buccal cavity.

The Labella.

The labella are oval lobes, separated from one another by a median fissure which extends throughout their anterior surfaces, and is there continuous with the groove on the anterior surface of the labium, but which is incomplete behind. The two labella represent portions of the second maxillæ which have remained distinct while the rest of the appendages have united to form the labium. Each lobe has an outer and an inner wall, the outer being composed of thin plates of chitin with membraneous intervals, the inner of the highly specialised pseudotracheal membrane, by means of which the fly absorbs its food. The structure of this membrane is familiar from many descriptions, and full details of its minute anatomy and mechanism will be found in Graham-Smith's recent paper, so that it will be unnecessary to discuss it here, especially since it is one of the first portions to disappear in the evolution of the blood-sucking proboscis. The outer walls impart the necessary rigidity to the labella, and have the chitin concentrated towards the periphery where the inner and outer walls join one another; at the anterior and posterior parts they bear a large number of pigmented macrochætæ, which project forward as a fringe distal to the organ.

There are two sclerites which support the labellar walls and at the same time unite the labium and labella, forming joints which permit of free movement between the two parts in an antero-posterior direction. The posterior of these is known as the *furca* (Plate II., figure 3). It is shaped like a rather wide horse-shoe, and embraces the posterior half of the labella. The posterior half of the arch fits between the arms of the fork of the mentum, the short transverse part lying opposite the incision between them. The furca is intimately fused with the external labellar wall, and is also attached to the membraneous portion of the wall of the haustellum in the region of the fork of the mentum, so that when it is swung backwards and forwards between the arms of the fork it carries the labellar wall with it; there is in addition a small heart-shaped piece of thin chitin attached to the transverse part of the arch, which passes downwards in the middle line behind, and further assists the furca in its control over the labella. The anterior or *discal sclerite* (Plate II, figure 4, Plate V, figures 27 and 28) lies between the labella, and is attached to the labial gutter. Its shape and position are of great importance from the comparative point of view, as it undergoes important modifications in the blood-sucking forms.

It is a racket-shaped loop of strong and heavily pigmented chitin, the broad distal end of which forms the margin of the oral pit, while the proximal end, corresponding to the handle, gives attachment to an important pair of muscles. The distal end is shaped like an isosceles triangle, forwardly directed and with rounded lateral sides and posterior angles; the base is incomplete in the middle third, the remaining portions projecting inwards as thin flanges. Anticipating subsequent descriptions, this portion of the *discal sclerite* may be called the *axial apophysis*, a term used by Stephens and Newstead in their description of the proboscis of *Stomoxys*. The proximal portion of the sclerite consists of two strong rods, which arise from the thickened posterior angles, and pass backwards, at first parallel to one another, but diverging slightly towards their ends; they are about equal in length to the axial apophysis. When examined in profile it is seen that they are not quite in the same straight line as the distal portion of the sclerite, but are curved a little upwards as they diverge from one another. These portions of the sclerite may be termed the *labellar rods*.

The position of the discal sclerite will be better understood by reverting for a moment to the structure of the labium as a whole. It is essentially a hollow organ, the chitinous and membraneous walls of which are continuous throughout the labium and labella, and enclose a space in which are contained the muscles which move the labella, some tracheæ, and a labial salivary gland, all of which lie in the hæmatocœle, a space continuous with the hæmatocœle of the head and body of the fly. At the distal end, where the labium is divided into the labella, it is invaginated, and so presents a double contour on cross-section, the two opposing inner walls being the pseudotracheal membranes. The discal sclerite is situated in the apex of the invagination, and the converging lateral halves of the membrane are attached to the margins of its expanded distal portion, all the channels terminating around this point. The aperture enclosed by the sclerite is therefore the commencement of the food canal and may be termed the *prestomum*. The mouth, as already pointed out, lies at the distal end of the buccal cavity.

The discal sclerite is attached to the two lateral rods which form the sides of the labial gutter by short tendons, which pass from the attenuated ends of the rods to the thickened posterior angles at the junction of the parallel with the curved portions of the sclerite. Their attachment functions as a joint, and the discal sclerite can be rotated on the fixed point through an angle of ninety degrees or a little more; in the closed position the labellar rods lie distal to and in the same line as the labium; when the labella are expanded for use they are rotated so as to lie perpendicular to the labium, and therefore parallel to the surface on which the fly is feeding.

The *prestomal teeth* (Plate II, figures 6, 7 and 8), though of only secondary importance in the economy of the house fly, have a special significance from the comparative point of view as being the homologues of the powerful cutting teeth of other Muscids. They are situated around the periphery of the prestomum, their proximal ends being attached to the discal sclerite and their distal ends directed outwards. The number and arrangement differ a good deal in nearly allied species, but they always conform to the same general type. Those of *Musca domestica* have been described by Kraepelin, and those of the Blow-Fly by Graham-Smith. The arrangement in *Musca nebulo* resembles the above. In *Musca convexi frons* it is somewhat simpler, as there is only one row of teeth, and only four on each side. Their disposition in this species is represented in figure 8, Plate II, where these are shown in side view, the terminations of the pseudotracheal channels being also indicated. Each tooth is a small petal-like slip of yellow chitin, contracted at its base to a rounded cord and expanded and hollowed distally into a shallow trough. The inner end is articulated to a thin raised flange of the discal sclerite, and the inner half of each tooth is adherent to the membrane between the pseudotrachae; the distal margin is irregularly serrated, but on account of the extreme thinness of this part of the tooth it is difficult to make out the precise outline.

The terminations of the pseudotracheal channels at the prestomum are somewhat peculiar. As the channel approaches the orifice the rings develop a median inward projection, so that when seen in optical section they appear T-shaped instead of straight; in the last complete ring this spur is produced inwards almost to the margin of the orifice, though it does not appear to be actually attached to it. On either side of the end of the channel, and embracing the last ring, there are several curved filaments of chitin which unite to form a thick strand, those of two sides passing inwards in contact with one another, between the teeth, to be inserted into the flange on the discal sclerite.

The Musculature and Mechanism.

It is not necessary to give here a detailed account of all the muscles and other structures which are concerned in the mechanism of the proboscis, but rather to indicate the main features of the movements and the musculature, so that the modifications found in the blood-sucking members of the group may be compared with the *Musca* type. The muscles are extremely difficult to study, and the chances of making an error with regard to their exact points of attachment are so great that it would not be worth while to attempt to describe minor differences. A full account of the different muscles and their actions will be found in Kraepelin's paper.

The first movements to be considered are those which result in the extension and retraction of the proboscis; as already stated, the whole organ is drawn up underneath the head when not in use, and can be extended into a straight line perpendicular to the long axis of the body when required. The labella also can be folded and expanded. The movement has to be considered joint by joint, though it must be remembered that in life all the joints are moved at the same time, the extension and retraction taking place rapidly. The extension of the rostrum on the head is brought about by a rotation of the fulcrum on the anterior border of the epistomal orifice, in such a way that its lower end passes forwards and downwards. The motive power for this is to be found in the distension of the large air sacs which lie on either side of the fulcrum, the air being expressed from the body of the fly into the head by means of the respiratory movements of the fly, as described by Kraepelin. The rostrum is extended, in fact, much as one would straighten the finger of a glove by blowing into it. The extent of possible movement is approximately rotation through a right angle, from the horizontal to the vertical position. Extension of the haustellum on the rostrum is accomplished mainly by the contraction of the muscles which are attached to the apodemes of the labrum, passing between the expanded upper ends of the apodemes and the lower end of the fulcrum; they pull in a downward and inward direction, and so force the labrum, and with it the labium, into line with the rostrum, by straightening the two at the loose joint in the region of the buccal cavity. The actual point on which the rotation occurs appears to be the membraneous union between the epipharynx and hypopharynx and the small chitinous plate which forms the walls of the buccal cavity.

The movements in these two joints by which the proboscis is retracted are both produced by muscular action. The fulcrum is rotated upwards and backwards by means of two pairs of muscles. The anterior pair of these is short, and passes between the internal surface of the head capsule, at a point just below the antennae, and the prominent posterior horns of the fulcrum; its action causes the fulcrum to rotate on the fixed point provided by the pressure of the anterior arch against the anterior edge of the epistomal orifice. The posterior muscle is very long, and passes between the internal surface of the head capsule in the region of the occipital foramen and the upper border of the mentum. The two act together, and the fulcrum, and with it the rest of the rostrum, is drawn upwards as it is rotated. The folding of the haustellum on the rostrum is accomplished by means of certain groups of muscles lying on the anterior surface of the rostrum; these are somewhat ill-defined, and many separate muscles which may fulfil this function have been described. The most important ones appear to be a pair which pass between the distal

ends of the labral apodemes and the anterior arch of the fulcrum, and act in the reverse direction to those which are inserted into the expanded ends of the apodemes.

These two joints provide a very wide range of movement, and the distal end of the labium may be moved to any point within a segment of a circle the centre of which is situated at the point of attachment of the rostrum to the head, and the radius the length of the organ in the extended position. The upper limit of this segment is in the horizontal plane, a little below the line of the long axis of the body; the posterior limit is the vertical line between the epistomal orifice and the surface on which the fly is feeding. The joints do not permit of any lateral or rotatory movement.

The movements of the labella are somewhat complex, but as these organs become fixed and greatly altered in the blood-sucking flies, a brief note will suffice here. The movement is of two kinds, produced by different forces, and brings about very marked changes in the form and position of these organs. In the normal resting position the labella are compressed, and their two walls are separated from one another by only a small amount of cellular tissue. The two lobes are folded backwards on the end of the haustellum, rotation taking place at the joint between the end of the labial gutter and the discal sclerite, and between the fork of the mentum and the furca. The distal margins of the outer walls of the two labella are in contact with one another, and the oral surface is completely concealed. When they are required for use they are distended with blood from the hæmatocœle of the labium, which is of course in direct communication with the rest of the body cavity, in such a way that their internal surfaces are forced apart, and the outer walls rotated outwards and upwards as the space between the internal and the external wall of each labellum is increased. At the same time the discal sclerite and the furca are rotated by muscular action, so as to bring the expanded surface, which has now been formed by the two internal walls, into a position at right angles to the rest of the proboscis in its extended position.

The muscles which produce these actions are found in the blood-sucking flies in very much the same arrangement as in *Musca*. There are three main groups, two longitudinal and one transverse. The transverse muscle is comparatively small, and is found only in the lower part of the labium; it runs on each side between the internal surface of the mentum and the labial gutter, and by reducing the transverse diameter of the labium tends to drive the blood into the labella when they are to be distended. The anterior and median of the two groups of longitudinal muscles, arising from the mentum in its upper part, is inserted into the labellar rods of the discal sclerite, and on contraction rotates them backwards at the joint formed by its attachment to the ends of

the labial gutter. The posterior and lateral group of muscles becomes of very great importance in the more highly specialised flies. It arises together with the retractors of the discal sclerite, and is inserted into the arms of the furca. As one pair of these muscles is inserted into the anterior and the other into the posterior of the two sclerites which connect the labella with the labium, the two are antagonistic; when they act together they will spread out and stretch the labellar walls, and when they act independently one will erect the labella and the other, the one attached posteriorly, will bring the labella to the position of rest. Both acting at the same time will retract the labella, and will therefore antagonise the transverse muscle, which by driving the blood distally will tend to distend them. The distension of the labella is not, however, due entirely to the action of the transverse muscles, but is helped by the muscles of the abdomen acting as in respiration; the longitudinal muscles of the labium have to antagonise the transverse muscles to the extent of driving the blood from the oral lobes, when the proboscis is to be retracted.

The evagination and invagination of the labella in *Musca* should be particularly noted, for it furnishes the clue to the mechanism of the biting apparatus of the blood-sucking flies of this group, in which the undoing of the evagination between the walls of the labella, by which the internal surfaces become external, constitutes the act of biting.

The prestomal teeth of the house fly are probably used to scrape food surfaces, and are moved by the alternate contractions of the anterior and lateral muscles, which cause the discal sclerite to rotate in an anterior and posterior direction on the pivot formed by its attachment to the labial gutter. When they are in use the posterior portion of the wall is drawn backwards out of the way by the muscle attached to the furca; as only the distal half of each tooth is free from the membrane, they cannot be very efficient weapons, but in view of the homology existing between them and the powerful teeth of other flies their method of action is interesting.

The Development of the Blood-Sucking Habit.

While the domestic species of *Musca* are mostly omnivarous, it is a matter of common knowledge that they are especially attracted by animal juices, either excrementa or exudations from the living body. Any slight cut or abrasion of the skin is certain to be sought out, and in the case of sick animals, too weak to protect themselves with their tails, flies collect in enormous numbers, especially in tropical countries, to feed on the exuded fluids. The prestomal teeth are probably sufficiently powerful to scrape away coagulated serum so as to enable the fly to reach the moisture beneath, though not to cut through living tissue. It is not unreasonable to infer that, in the ordinary

course of evolution and differentiation of species, certain forms arose which had a special taste for blood and at the same time specially strong prestomal teeth, by means of which they were able to scrape an abraded surface more effectively, and, in a further stage, to make a wound on unbroken skin. Once such a habit was started it would be only a matter of time until the fly became confirmed in this manner of obtaining food, and in succeeding generations the whole structure of the proboscis would become adapted for this specialised function, the separate stages of the process remaining as distinct forms, more or less predominant and widespread according to the degree of perfection of their adaptation to their environment.

It so happens that these theoretical considerations receive confirmation from the study of the habits of some members of the genus. There are at least three flies, and probably many more, which, although their teeth are no more powerful than those of *Musca nebulo*, are nevertheless confirmed blood-suckers, and probably have no other food. These are *Musca corvina*, Portchinski, *Musca pattoni*, Austen, and *Musca convexifrons*, Thompson. The two latter are both common cattle flies in Madras, and have the peculiar habit, first pointed out by Captain Patton, of feeding on the blood which exudes from the wounds made by true biting flies, most frequently associating for this purpose with *Philæmatomyia insignis*, the commonest biting fly in this district. Both these flies are much larger than *Philæmatomyia*, and it is very remarkable to watch them, often half a dozen at a time, collect round the smaller fly as it is in the act of feeding, and endeavour to thrust their proboscides near the wound. As soon as the biting fly has finished its meal and flown off, one of the others takes its place and at once settles down to feed, only leaving the wound when it is as fully gorged as possible; both these flies resemble true biting flies in taking at one meal the maximum quantity of blood that they can contain.

These three flies, then, are examples of an early stage of the development of the blood-sucking habit; closer observation of the habits of other species in other parts of the world will probably reveal many instances of this peculiar form of parasitism. The matter is one of considerable economic importance, for such flies are as capable of transmitting blood parasites as those on which they rely for food.

The presence of even minute prestomal teeth is worthy of consideration when dealing with the question of trypanosome transmission, for it has been repeatedly shown that the discharge from ulcers, which are so constant a

N. B.—Since writing the above, another species which has the same habit has come to light. This fly, which has the additional peculiarity of being larviparous, has been described by Captain Patton and myself under the name of *Musca bezzi*, in a paper in the Indian Journal of Medical Research, Vol. I, No. I.

feature of many trypanosome diseases, contain large numbers of trypanosomes. Any such delicate organism would die after a very short exposure to the air and to the tropical sun, but flies with teeth sufficiently strong to scrape away the protective clot so as to reach the moisture underneath would be quite capable of transmitting live trypanosomes from one animal to another.

The Structural Changes in the Proboscis.

Before considering the different forms in detail it will be of advantage to indicate briefly the directions in which the structural changes, which are the response to the change in the habit of life, are to be looked for. All the modifications can be traced to the development of the prestomal teeth, the increase in the size and importance of which has rendered necessary a corresponding increase in the stability of the structures which support them, and in the strength of the muscles which bring them into play. At the same time the proboscis is altered in shape in such a way that it has actually become a piercing organ, pointed at the distal end and able to enter the skin of the host, in some cases to a considerable depth; and as the piercing parts are limited to the haustellum, this part of proboscis has become elongated, until it may be, as in *Glossina*, more than three times the length of the rostrum. The muscles which actuate the biting apparatus, greatly increased in size, are collected towards the posterior end of the labium, and connected with their insertions by tendons. At the same time the pseudotracheal membrane, no longer of use to the fly, has disappeared. The anterior of the two joints by which the labella in *Musca* are articulated to the labium is fixed more or less firmly in that position in which the labella are in a line with the labium. The discal sclerite is separated into two parts, the axial apophysis and the labellar rods, to the latter of which the teeth are attached by means of a projecting flange. The rods themselves are expanded into plates forming an incomplete collar round the prestomal orifice. The furca, to which the powerful muscles which move the teeth are attached, is greatly thickened, and takes part in a much more definite articulation. The fork of the mentum is resolved into its two parts, the distal one of which is moved forwards and outwards and takes little or no part in the articulation. The most obvious change is in the position of the proboscis in the resting attitude. On account of its increased length the haustellum can no longer be concealed when it is retracted, and projects conspicuously in front of the head.

The pseudotracheal membrane of *Musca*, as pointed out by Graham-Smith, fulfils a special function in filtering the food of the fly so as to prevent the ingress into the food canal of particles too large for its lumen. In the biting flies the membrane no longer exists as such, but some sort of filter is

as necessary in these flies as in the non-biting ones, for on account of the method by which the wound is made there must be many particles, torn off by the teeth, sufficiently large to block the canal between the epipharynx and the hypopharynx if they gained access to it. This is prevented by the development, from the remains of the rings of the pseudotracheæ, of a series of processes, which are attached between the teeth and are swept through the wound in advance of them to keep clear the surface to which they are applied.

The Genus Philæmatomyia.

The genus *Philæmatomyia* was created by Austen in 1909, for one species, *insignis*. The characteristic feature of the genus is the presence of a circlet of teeth at the apex of the proboscis, between the labella. In other respects it closely resembles *Musca*, and unless the teeth are noticed there is nothing about the general appearance of the proboscis to suggest that the fly is a blood-sucker; it is probable that the above species, which appears to be widely distributed and common where it occurs, had previously failed to attract notice on account of its innocent and inconspicuous appearance.

Since the description of the above species two others have been found, *viz.*, *Philæmatomyia lineata*, Brunetti, and *gurnei*, Patton and Cragg. Both these, and especially the latter, appear to be rare flies, at least in Madras, where *insignis* is extremely common. All three are of exceptional interest, as they represent separate and early stages in the evolution of the blood-sucking proboscis. In all the proboscis is of the simple *Musca* type, is completely retractile within the head, and possesses a pseudotracheal membrane: the relative proportions of the rostrum and haustellum are the same as in *Musca*, the labella are only a little reduced in size, and the hairs and macrochætæ are similarly distributed and fairly abundant. It is obvious that such a proboscis cannot be simply thrust into the skin of the host, and, as will be seen when the mechanism is discussed, the wound made is a scarification rather than a puncture. The teeth are used, in fact, very much in the same way as those of a non-biting *Musca*.

The structure of the proboscis being for the most part identical with that of *Musca*, it need not be described in detail, and we may proceed at once to consider the modifications which are found. They are all in connection with the teeth, the discal sclerite, and the labial gutter; it will be convenient to deal with each fly separately.

Philæmatomyia lineata.

The evidence with regard to the blood-sucking habit of this species requires confirmation. In Brunetti's original description it is stated that Dr. Annandale

has seen it gorged with blood, but this is not absolute proof that it can itself make an effective wound, for it may have the same habit as *Musca pattoni* and *convexi frons*. It is not common in Madras, and neither Captain Patton nor myself has been able to confirm Dr. Annandale's observation, or to ascertain if it can make a wound for itself, though we have frequently seen it on cattle.

The *teeth* (Plate IV, fig. 24) are shaped like rose thorns, and are attached to the membraneous inner wall of the labella by expanded bases, as thorns are attached to a stem. When seen in profile it is evident that only the distal half of each tooth is free from the membrane; the middle portion is composed of a slightly expanded base; the proximal portion of the tooth is flattened, adherent to the membrane, and distinctly divided in its long axis, so that it consists of two lateral ribs with a thinly chitinised interval between them; these are articulated to a flange of the discal sclerite.

There are four of these teeth, similar to one another in size and shape, situated at the prestomal orifice, and alternating there with the terminations of those pseudotracheal channels which open directly into the prestomum. The pseudotracheæ do not extend quite so far inward as do the corresponding ones in *Musca*, but terminate at the level of the distal portion of the attached bases of the teeth. On each side of each channel there is a pair of narrow flattened chitinous strands, which unite with those of the opposite sides to form a thicker strand at the level of the separation of the tooth from the membrane. This strand is continued between the teeth to near the attachment of the inner wall of the labellum to the discal sclerite, there being one such strand between each two teeth and one on the proximal side of the proximal tooth. At the distal side of the four large teeth there is a smaller thin slip of chitin, which appears to represent a rudimentary tooth. It is situated at the point where the anterior collecting channels terminate, and is contiguous with the irregularly shaped plates of chitin which replace the rings of the collecting channel in this region.

The *discal sclerite*, though retaining the general shape and appearance of that of *Musca*, shows evidence of the commencement of important changes. In the first place, it is much stouter and more heavily pigmented than in the non-biting species, to correspond with the increased size of the teeth and the necessity for more powerful muscles. The racket shape is modified by the wide separation of the labellar rods, with the result that the sclerite is V-shaped, the point corresponding to the junction of the parallel rods with the loop in *Musca* being marked by a prominence on the external surface.

The separation of the discal sclerite into two portions is evident even at this early stage. If a well cleared preparation (Plate V, fig. 31), carefully decolourised with chlorine, be examined under a high power, it will be seen

that there is a definite fissure separating the anterior fourth from the posterior three-fourths, commencing on the external surface a little below the pointed apex and running backwards and slightly outwards towards the inner surface. The portion anterior to this fissure is the axial apophysis, and that posterior to it the labellar rod; the importance of this distinction will be seen later.

The *axial apophysis* is Y-shaped, the long arm of the Y, free and forwardly directed, being the most distal part of the sclerite; the lateral arms are only separated from the labellar rods by the fissure described above. The distal part is not straight, but is bent forwards at a right angle, so that its extremity lies in approximately the same plane as the teeth when extended for use; it is interesting to note that in decolourised preparations a median fissure separating the axial apophysis into two lateral halves can be made out.

The *labellar rods* consist of three parts, a posterior part in which the muscles are inserted, an anterior part which unites with the axial apophysis, and a tooth plate. The posterior portions, composing about half the length of the sclerite, are wedge-shaped and have their pointed ends directed outwards and backwards; their broad ends form prominent tuberosities on the outer sides of the sclerite. The anterior part is thinner and somewhat flattened from side to side. The tooth plate is a narrow flange of thin chitin, arising from the whole length of the outer edge of the anterior portion of the sclerite and following its curve; it is continued in front of the fissure separating the axial apophysis from the labellar rod, but at the fissure it turns directly forwards as an isolated spur, which reaches to about the level of the tip of the apophysis. It is from this spur that the rudimentary tooth arises. Posteriorly the flange is continued inwards and upwards across the tuberosity, the most posterior portion projecting inwards towards that of the other side. When seen in profile the tooth plate presents a sickle-shaped free border, the anterior and posterior extremities of which are placed at the terminations of the two longitudinal collecting channels of the pseudotracheæ. The bases of all the teeth and the terminations of the central pseudotracheæ fit into the concavity, and the proximal ends of the teeth and the supporting strands of the pseudotracheæ are attached around its margin. In this way the tooth plates of the two sides form a sort of cup into which the bases of the teeth fit.

The *labial gutter* of this species differs from that of *Musca* in the greater thickness and pigmentation of its chitin. The lateral rods are definitely demarcated, and articulate with the labellar rods at the junction of the anterior and posterior portions. They can be traced almost to the proximal end of the mentum, lying on either side of the labrum-epipharynx. *The hypopharynx is free from the gutter except at the extreme upper end.*

The *pseudotracheal membrane* does not differ from that of *Musca*. There are, however, only eighteen channels, whereas twenty six seems to be the average number in non-blood-sucking forms.

The mechanism of the proboscis appears to be identical with that described for *Musca nebulo*. The teeth are brought into play by the contraction of the muscles inserted into the furca, the requisite resistance and adaptation being obtained by the muscles inserted into the labellar rods. When in use the labellar rods are placed more or less perpendicular to the labium, and the teeth, turned outwards by the tightening of the membrane to which their bases are attached, are arranged in a half moon with the axial apophysis in the centre, not in a circle as stated by Brunetti. They may either be drawn across the surface in an antero-posterior plane by the movement of the labellar rods on their attachment to the labial gutter, or they may cut by the simple eversion of the labellar walls, which turns them outwards and at the same time draws their points across the skin.

Philæmatomyia gurnei.

In a recent paper written in conjunction with Captain Patton of this Institute the discovery of this species was briefly chronicled, a detailed description being deferred in the hope of obtaining more material. Unfortunately this hope has not been realised, and up to the present time the only specimen in our possession is the one from which the original description was given.* It happened, however, that this specimen was caught in the act of sucking blood from a cow, and had its abdomen distended with blood, so that there is no doubt regarding its habits. The proboscis was removed from the head, cleared in potash, and partially dissected so as to display the teeth and connected structures. The discal sclerite, separated from the labium by the rupture of its tendinous attachment to the end of the labial gutter, was flattened out and compressed, in order to display the teeth of both sides, and in doing so the attachments of the axial apophysis to the labellar rods were fractured and the pseudotracheal membrane and part of the outer wall of the labella, torn. The microphotograph (Plate V, fig. 32) represents the appearance after this dissection.

The *teeth* are much stouter and shorter than those of *lineata*, though they resemble them in general configuration; their greatest breadth is about one-fourth the length. There are five principal and threc rudimentary teeth on each side, arranged in a similar manner to those of *lineata*; the large teeth are

* A series of this species has been obtained while this Memoir was in the press. A detailed description appears in the Indian Journal of Medical Research, Vol. I, No. 1. Examination of further specimens has confirmed the above account.

in the middle, and on each side there is another similar in shape but only about one-fourth the size, and on the inner side, internal to this, there is a small slip which may be taken as a rudimentary tooth. As in *lineata*, only the distal half of each tooth is free from the membrane; at the extreme tip there is a series of rather coarse serrations. The serrated edge must be directed upwards when the teeth are everted. The proximal ends of the teeth are distinctly bifid. They are not directly attached to the tooth plate.

Between the teeth there are certain structures (Plate II, fig. 9) simple in this species, but assuming an extraordinary complexity in the more differentiated forms, which may be termed generally the *interdental armature*. They occupy the position of the Y-shaped strands of chitin which support the terminations of the pseudotracheæ in *lineata*, though they, like the teeth, are not attached to the tooth plate directly. They consist in this species of small leaf-like plates of chitin, arranged in pairs, one pair between each two adjacent teeth. The two blades of each pair are turned slightly inwards towards one another, so as to enclose between them the end of the pseudotracheal channel. The blades are about the same length as the teeth, and arise from the membrane by short stalks; the extreme tip and the edge most distant from the pseudotracheæ are thicker than the rest of the blade.

There are twelve pseudotracheal channels, arranged in the usual manner, except that the anterior and posterior collecting channels are each only continuous with two pseudotracheæ, the remainder terminating directly at the prestomum. There is a slight difference in the method of termination; the rings, instead of having inwardly directed projections, are split into two halves, and each half is turned inwards towards the tooth plate, one being in advance of the other so that they appear to alternate.

The *discal sclerite* shows a further advance in specialisation both in the degree of separation of the two constituent parts and in the thickness of the chitin. The *axial apophysis* is a stout conical piece of very deeply pigmented chitin, about twice as long as broad, and produced distally to a sharp point; it lies between the anterior ends of the labellar rods, and is fused with them in the posterior third of its extent. The apex of the apophysis is situated on a level with the bases of the pair of teeth nearest the middle line, so that when the teeth are turned outwards its point must project beyond them. The *labellar rods* consist of two portions differing greatly in the thickness of the chitin; the posterior portions are stout wedge-shaped rods bent slightly outwards from one another and terminating in blunt and rather thinner ends; they therefore closely resemble the corresponding parts of the sclerite in the last species. The expanded distal ends of these rods extend much further on the outer than on the inner side, so that the rods are triangular, with two nearly

equal sides and one long one externally. The distal side of this triangle is produced forwards and inwards into a thinner sheet of chitin, roughly quadrilateral in shape, which is fused internally with the axial apophysis, and to the distal margin of which the tooth plate is attached; this flattened sheet corresponds to the distal curved portion of the sclerite in *lineata* and to the horse-shoe shaped arch in *Musca* (the extreme tip excepted).

The *tooth plate*, as seen in the flattened preparation, is a thin sickle-shaped slip of yellow chitin arising from the distal margin of the labellar rod on each side. The anterior portion, corresponding to the handle of the sickle, occupies about one-third of the length, and is directed straight forwards, those of the two sides being approximately parallel to one another, and situated on either side of the axial apophysis. They are attached to the labellar rods at their proximal ends, the rest of their periphery being connected only with the membrane forming the inner wall of the labella. The middle third of the plate is not distinguishable from the margin of the rod, but the posterior third extends forward and outward to about the level of the tip of the axial apophysis. In this way the tooth plate of each side forms a hollow cup into which the bases of the teeth fit, though *in this case without any chitinous attachment.*

The *labial gutter* in this species appears for the first time as a definite isolated structure, very different from its inconspicuous homologue in *Musca.* It is a thick and heavily pigmented rod, running the whole length of the labium, and composed for the anterior two-thirds of its length of much thicker chitin than any other part. The lateral margins of the gutter are separated from the middle portion by a narrow area of thin chitin; they do not reach quite to the upper end of the labium, but merge with the base of the hypopharynx and the adjacent membrane, which connects them with the mentum. The median groove, so far as can be judged from a specimen mounted on its side, is of considerable depth; like the lateral portions, it is thinnest at the upper end.

On the posterior surface of the gutter there is a median backwardly projecting ridge, commencing about the middle of the gutter and increasing in width as it passes upwards, but at the same time becoming thinner, until it is lost in the neighbourhood of the base of the hypopharynx. This is the " keel ", corresponding to the structure in *Stomoxys* described by Stephens and Newstead. It projects backwards into the cavity of the labium, dividing it into two lateral halves, and is developed to provide additional attachment for an important group of muscles. Its significance will be shown in connection with the next species, in which it has been more closely studied, and it will be sufficient to note here its occurrence and extent.

The distal end of the gutter, where it articulates with the discal sclerite, is apparently moulded to form a joint. On the posterior surface there is a deep notch, caused by the extension of the lateral rods beyond the median portion of the gutter; the extremities of the sides of this notch are indented, and project forwards in their most anterior parts. There is no continuous chitinous union between the end of the gutter and the discal sclerite, and it looks as if the two were articulated by this simple joint to permit of free movement; under a high power the slightly projecting internal angles of the posterior portions of the labellar rods can be seen to be distinctly moulded so as to fit into the notch on the end of the labial gutter. The wide separation between them as shown in the drawing is of course an artifact due to the splitting of the sclerite by pressure.

The *mentum* shows some modification in this species as compared with the preceding. It is deeper, narrower, more capacious at its proximal end, and more pointed distally. The arms of the fork of the *mentum* are not so long, and the distinction between the two joints of the fork cannot be made out in my specimen. The *furca* is somewhat rounder and stouter, and is distinctly thickened in its middle portion, where it lies between the arms of the fork.

Philæmatomyia insignis.

The structure of the proboscis of this fly has already been fully described in a previous memoir, and it will only be necessary to recapitulate such points as have an importance from the present point of view. It is the most highly specialised of the genus, and we may note in passing that it is, so far as is known at present, also much the most common and widely distributed one. In Madras it is quite the most common biting fly found on cattle, and an idea of its prevalence may be gathered from the fact that one can frequently count twenty or thirty specimens on a single cow. It would be almost justifiable to infer that whereas the two previously considered members of the genus have not advanced sufficiently far to adapt themselves with success to an exclusively blood-sucking habit, and have at the same time become less fitted to obtain food in the manner usual in Muscids, this species has succeeded in establishing itself, and has become predominant.

In external appearance this fly differs no more from *Musca* than do the other species. Its proboscis is as completely retractile and is blunted at the tip, and the only suggestive thing to be noticed about it is its attitude when feeding. Instead of moving about the skin of its host, it settles down in a crouching attitude and remains on the same spot till obviously gorged with blood, all its legs bent and its head depressed, in an attitude very like that assumed by *Stomoxys*. This species appears to take no food other than blood, and

it is somewhat remarkable that the pseudotrachael membrane should be retained in an apparently functional condition, co-existing with a biting apparatus which, as the anatomy of the parts and the observed habits of the insect both go to show, is an extremely efficient one. It is possible that the membrane is used in the same way as that of *Musca*, when the fly sucks up the blood from the wound.

The changes from the Muscid type are all found in the labium and the labella. In the rostrum all that can be distinguished is the relatively rather shorter length, and some elongation of the buccal cavity, the sclerite composing the walls of which is more pointed than in *Musca*, and curves over a little more laterally. The teeth are reduced in number and increased in size and strength, and are fitted more closely to the end of the discal sclerite. The discal sclerite itself shows complete differentiation into its two parts, and a definite change of form, the object of which is to render the joint between it and the end of the labial gutter more compact, and to fix the bases of the teeth more firmly. The method of attachment of the teeth should be particularly noted. Their bases are not attached to the sclerite, but lie in a cup formed by the projecting flange termed the tooth plate, the bases of the two smaller teeth at either end of the set on each side being a little in advance of those of the larger teeth, so that although the teeth are unequal in size their apices are in approximately the same line, while their bases form a concave line corresponding to the shape of the cup in which they fit. Owing to the alteration in the shape of the sclerite the teeth are attached to its distal end, and are directed downwards when the labellar rods are in the same line as the labium, whereas in *Musca* the teeth are directed downwards when the discal sclerite is perpendicular to the labium. As a consequence of this the axial apophysis now points in the same direction as the teeth when they are not everted; when they are spread out it forms the most distal part of the proboscis, and it is possible that it is used as an accessory tooth, or perhaps as a fixing point when the teeth cut by eversion. The interdental armature, inconspicuous in the other two species, reaches a high stage of development in the serrated blades, while the pseudotracheal membrane is distinctly smaller than one would expect from the size of the fly; the rod-like hairs make their first appearance in this species. The labium shows a high development of the labial gutter, and changes, such as the narrowing at the lower end of the mentum, the consolidation of the joint between it and the furca, and the thickening of the latter, which indicate an approach to the *Stomoxys* type of piercing proboscis.

Summary of the Genus Philæmatomyia and its relations to Musca.

We have in the genus *Philæmatomyia* a series of three flies which mark different stages in the adaptation of the Muscid type of proboscis to a

blood-sucking habit. Notwithstanding the fact that the last member of the group is a voracious blood-sucker, and has, so far as I have been able to ascertain by a close observation of its habits and by repeated examinations of its intestinal contents, no other food than blood, there is no change in the external appearance of the proboscis, and the existence of biting parts may be unsuspected until they are revealed by dissection ; the proboscis retains its retractility, and is withdrawn in a typical Musca-like manner when not in use.

The changes from the *Musca* type fall into three groups ; those dependent on the increase in the size and in the functional importance of the teeth, those in the pseudotracheal membrane, and certain modifications in the general form of the proboscis. These latter are inconspicuous and will be referred to later in connection with the more marked changes of a similar nature found in the *Stomoxydinæ* and in *Glossina*.

In addition to the increase in size, the teeth show a tendency to an approximation of their bases. As this occurs, the flange of the discal sclerite which supports them develops into a cup, formed by the flanges on the two sides and situated at the distal end of the sclerite, into which their bases fit. In *Musca* the proximal ends of the teeth are attached directly to the chitinous margin of the prestomum, but in the last two species they are quite free from it, being attached only to the membrane on the inner wall of the labellum, and held in position by the flange; this facilitates eversion.

The discal sclerite is separated into its two parts, the axial apophysis and the labellar rods, to an increasing degree in the three species; at the same time the parts change their shape and their relations. Comparing the two extremes, as seen in *Musca* and in *insignis*, we find that there has been a backward displacement of the axial apophysis, or, what is the same thing, an elongation of the labellar rods, and that at the same time the attachment of the teeth to the discal sclerite has passed from the sides of the sclerite to the distal end. In *Musca* the teeth are attached to that side of the sclerite which is distal when the oral lobes are distended for use and the sclerite perpendicular to the labium, but in *insignis* they are situated at the end of the sclerite, which can only be distal in position when the labellar rods are in the same line as the labium. In each case the teeth are arranged around the incomplete chitinous ring which is formed by the discal sclerite at the prestomum, but in *Musca* this is only directed downwards, in which position it must lie when the fly feeds, when the labellar rods are parallel to the food surface and therefore perpendicular to the labium, while in *insignis* the orifice is only open in a position at a right angle to this. There is therefore an alteration in the position of the discal sclerite, when the teeth are in use,

which amounts to a right angle, and we have to consider the causes which have brought this about.

It was stated in the account of the mechanism of the proboscis of *Philæmatomyia insignis* that the teeth cut by eversion, this being effected by the muscles inserted into the furca and acting on the teeth through traction on the inner wall of the labella. Now the relation of the size of the teeth to the extent of the inner wall is very different in *Musca* and in *insignis*, for in the former the pseudotracheæ are functional and the teeth rudimentary, while in *insignis* the membrane is reduced in size and complexity, and the teeth very large. It follows that cutting by eversion will be much more effective in *insignis* than it could be in *Musca*, though it probably does occur in the latter form. But the teeth of *Musca* can also be brought into action by alternating contractions of the anterior and posterior muscles, which rotate the discal sclerite in opposite directions on its point of attachment to the labial gutter, and such a movement will evidently be more effective than simple eversion on account of the greater range of movement of the teeth. Probably in *Musca* the two go on together. The teeth are first everted, the membrane drawn away, and the sclerite moved on its fixed point so that the everted teeth scrape the surface. As in succeeding generations new forms were evolved, the larger size of the teeth would make the act of eversion a more effective one in the scraping operation. But at the same time displacement of the teeth towards the distal end of the sclerite would be most advantageous to the fly, for it would shorten the arm of the lever to which the muscle is attached, and lengthen the one which bears the teeth, in this way giving to the cutting apparatus an increased facility for rapid action. We find then that in the three species of *Philæmatomyia*, contrasted with *Musca*, the teeth shew a progressive increase in size, closer approximation of their bases, and displacement towards the distal end of the sclerite. This is associated with a difference in the relation of the labellar rod to the labial gutter in the position of action, for in *Musca* the discal sclerite can only be rotated on its fixed point until it comes to a perpendicular position, whereas the sclerite of *insignis* can pass back until the labellar rods are in line with the labium, a position which would be of no advantage to *Musca*, but which gives a much longer range of excursion to the teeth in *lineata* and in *gurnei*, in the former of which the sclerite can certainly be brought more into line with the labium than it can in *Musca*. At the same time the joint between the sclerite and the end of the labial gutter has become consolidated, until in *insignis* we find the two parts definitely moulded to one another as a regular articulation. But in the latter species, the sclerite being in the same line as the labium, the teeth in their final terminal position, and the pseudotracheal membrane considerably reduced in extent, the

action of eversion of the teeth, brought about in the manner described, will be a most effective one. It is obvious that excursion through a short arc is more suitable for piercing, while a comparatively wide sweep of the teeth, such as would be obtained by rotation of the sclerite on its fixed point with the teeth in the everted position, is the better for scraping a surface. It is probable that scraping by rotation of the sclerite as a whole in an antero-posterior plane, through an angle of half a right angle or thereabout, with the teeth in the everted position, is the predominant factor in *Musca* and perhaps in *Philæmatomyia lineata*, while in the higher form which is exemplified in *insignis* the labellar rods are erected once for all at the commencement of the act of feeding, and the wound actually made by rapidly repeated eversions of the teeth.

In spite of the changes in the form and position of the sclerite the relations between it and the labella remain unaltered. The inner wall is attached to the borders of the sclerite as in *Musca*, and the interval between the two labellar rods corresponds to the median fissure on the anterior surface, between the two lobes. In order that the prestomal orifice may be directed distally, however, the labellar rods must be in line with the labium, not perpendicular to it. It should be remembered that the prestomum is not a closed ring, but is simply the point where the labellar walls converge to each other, and that it is defined by the discal sclerite. In *Musca* the opening through which food passes is at a right angle to the long axis of the sclerite, and *insignis* in its long axis, but in each case the interval between the labella is only closed in by the apposition of the two inner labellar walls.

The modifications of the labial gutter and the posterior joint are an obvious result of the method of action. The teeth and the discal sclerite are increased in size, and therefore require greater strength in the gutter which supports them; the increased weight and the more forcible movement demand greater consolidation of the joint and increased muscle, and this latter factor necessitates an increase in the area of muscle attachment, a demand fulfilled by the development of the keel. The posterior joint and its muscles also show an increase in strength and stability, in accordance with the greater importance of the muscles which evert the teeth.

Considerable interest attaches to the origin of the interdental armature, which, from its persistence in all the Muscid biting flies, is evidently an essential part of the biting apparatus. The key to its homology is to be found in a comparison of the two early forms with one another and with *Musca*, and in the relation between the degree of development which it exhibits and the extent of the pseudotracheal membrane. It was stated in the description of *Musca* that the method of termination of the channels of the pseudotracheæ

was variable, and the large amount of variation there is in even closely allied species is indeed remarkable. The variations are slight and difficult to make out, it is true, but it is just in such a labile structure that one would expect to find new developments. The usual method has already been described; the rings adjacent to the sclerite become more open, and develop a median T-shaped projection which is turned towards the prestomum. It is not actually attached to the chitinous margin, and on either side of it there are thin slips of chitin, sometimes simple, sometimes branched in an irregular manner, which pass from the sides of the open gutter at the termination of the channel towards the prestomum, and terminate either in very close proximity to it or by actually fusing with it. In some cases there appears to be a sort of loose joint between the two. These strands of chitin lie between the teeth and on either side of the gutter at their terminations; they are evidently of the same nature and origin as the rings of the pseudotracheæ, and are almost certainly formed by the splitting in the middle line of the terminal T-shaped rings. Now in *Philæmatomyia lineata* we find similar but much more conspicuous strands, arising from a common stalk between each pair of teeth, and dividing into four filaments terminally, two of these passing to each side of the end of the gutter. In *gurnei*, some of the last rings are divided into two, and pass towards the sclerite; outside these, and attached near the chitinous margin, there are two definite leaf-like blades, distinguished from the strands by their flatness, but otherwise disposed in precisely the same way. These are turned slightly outwards from one another at the distal end, where they lie on the sides of the terminal gutter of the pseudotrachea. In *insignis* the serrated blades, although elaborate, are essentially of the same nature as those seen in *gurnei*, and like them are derived from the proximal rings at the terminations of the pseudotracheal channels; each of the blades in each bunch represents a modified strand of chitin such as those in *gurnei*, attached to a common stalk, and the complexity of structure is more apparent than real. A comparison of the serrated blades of *insignis* with the chitinous strands which occur in the prestomal region of the blow-fly, as figured by Graham-Smith (his figure 8, *e.g.*) shows at a glance how the transformation has occurred.

The origin of the interdental armature from the pseudotracheal channels is all the more interesting when one considers the function which they fulfil in the two forms. As pointed out by Graham-Smith, the pseudotracheal channels of the blow-fly act as a filter to prevent the ingress into the mouth of particles too large for the food canal, and as I have shown in the case of *Lyperosia*, which is provided with an arrangement similar to that of *insignis*, the blades are swept across the wound in advance of the teeth at each eversion, and will thus keep the surface clear while the wound is being made. When it is

sufficiently large for the blood to flow, all the fluid which enters the prestomum must first have found its way through the network formed by the blades, which form a sort of brush at the extremity of the proboscis, an arrangement which must act as a most efficient filter. Thus, though the rings of the pseudotracheal channels have undergone a great change of form, the function is retained.

The affinities of the three species, so far as can be judged from the structure of their mouth parts, are as follows:—*lineata* is closely allied to *Musca*, while *gurnei* represents a much greater advance, and is probably the first stage at which the fly can make a wound for itself. *Insignis* is much further removed from *gurnei* than that fly is from *lineata*, as shown by the definitely erect position of the labellar rods in the position of action and the high degree of development of interdental armature. So far these are the only three species known, but it is highly probable that more will be found, as the first species described, *insignis*, has proved to be so common and so widely distributed since it was first differentiated from *Musca*. New species will be awaited with great interest, for among them one may expect to find forms showing intermediate stages, in which the teeth will not be quite terminal in position, and the discal sclerite not so much thickened nor quite in line with the labial gutter in the position of action. Such forms may also be expected to show stages in the evolution of the interdental armature midway between *gurnei* and *insignis*.

The Stomoxys Group.

The next three flies, *Hæmatobia*, *Stomoxys* and *Lyperosia*, are included in the *Stomoxydinæ*. The proboscis of *Lyperosia*, perhaps the most specialised of the group, has been described at length in a previous memoir, and in their main features the other two are so similar that no general description of them is necessary. The three flies studied in the present research do not present a connected series comparable with that formed by *Musca* and the genus *Philæmatomyia*, but there are certain points which appear to indicate that the order in which they are placed above is that representing their respective degrees of specialisation. There is a wide gap between these flies and those of the genus *Philæmatomyia*, but doubtless future research will reveal the existence of intermediate forms which will show the course of the evolution more precisely than it can be seen at present.

In view of the close similarity of these genera with regard to the structure of their mouth parts, a general account of the form of the proboscis in its relation to the Muscid type will be given first; the details in which they differ from one another, so far as they are cognate to the subject, will be given later.

All the changes from the *Musca* type are directed to one end the production of a piercing organ, to enable the fly to pierce the skin of vertebrate animals in order to suck their blood. The fundamental difference between the flies in this group and those of the genus *Philæmatomyia* is that they actually do pierce the skin, whereas *Philæmatomyia* only scarifies it.* The two essential features in such a piercing organ are that it should be rigid and that it should terminate in a point. It is in these directions that the proboscis in the *Stomoxydinæ* is altered from that of *Musca*.

Rigidity is obtained by the consolidation of the rostrum and the haustellum, the reduction in size of the former, and the closer linking of the two by means of the buccal cavity. The haustellum is greatly strengthened by the increase in the extent to which its wall is formed by the mentum, which curves forward so as almost to meet in the middle line in front, leaving only a narrow membraneous interval between it and the labial gutter. The teeth are also more closely united to one another, though still equally free to move in the socket formed by the tooth plate. The alteration in the attitude of the proboscis, which is the most striking feature, is merely due to the increased length of the haustellum, which can no longer be folded on the lower surface of the head, but projects horizontally forward when in the position of rest.

The movements of proboscis, though not so conspicuous as those of the house fly, are essentially the same, and have practically the same range. They are used to bring the proboscis from its horizontal position of rest into a more or less perpendicular position when the fly is feeding. On account of the alteration in the relative size of the haustellum and the rostrum, however, the latter is more or less fixed in the position of extension, and when the fly is at rest the two parts of the proboscis are at a right angle to one another; the rostrum is apparently capable of being moved in a forward direction to a greater extent than in *Musca*, and one can at times see the whole organ extended and pointing in a direction anterior to the perpendicular. One may note in passing that the arrangement of these joints is quite the least advantageous possible for the propagation of any force from behind, and that it is anatomically impossible that the piercing parts should be inserted by means of the muscular power of the body of the fly; the proboscis is merely lowered into the wound as it is made.

Rigidity is also produced by the consolidation of the anterior joint between the discal sclerite and the labial gutter, by the partial fixation of the labella in a position which corresponds to that of extension in *Musca*, and by the con-

* This does not mean that the proboscis of *Philæmatomyia* is necessarily a less efficient organ than that of *Stomoxys* and its allies. One may express the difference by saying that the one scrapes a hole in the skin, the other bores a hole.

solidation and modification of the posterior joint between the furca and the mentum.

The alteration in the shape of the proboscis is practically confined to the haustellum. This is always much broader in the upper than in the lower part, and tapers to a point anteriorly. The labella are so much reduced in diameter that they are little if at all wider than the narrowest part of the haustellum, and thus offer no obstacle when the proboscis enters the skin. The macrochætæ which are so conspicuous in *Musca* are reduced in number and in size, both at the distal margin of the labella and on the sides of the mentum.

The alteration in the appearance of the proboscis depends mainly on the progressive enlargement of the haustellum and diminution in size of the rostrum. This change in the relative proportions of the parts of the proboscis is a fundamental one, and can be traced through the whole group from *Musca* to *Glossina*. It forms a reliable index of the correct position of the several members of the group. The following are the proportionate lengths of the rostrum and haustellum in all the flies considered in this paper. In the case of the *Stomoxydinæ* the measurements were made along the posterior plate of the fulcrum from the upper to the lower cornua, and from the upper limit of the mentum to the tip of the labella, following the curve of the organ. In *Musca* and *Philæmatomyia*, an equivalent measurement of the haustellum was obtained by adding together the length of the labial gutter and of that portion of the discal sclerite which is distal to the articulation, including the teeth. The figures represent an average of several observations on different specimens; on account of the impossibility of obtaining a series of preparations mounted in exactly the same way they are to be regarded as roughly approximate only.

	Rostrum.		Haustellum.
Musca nebulo	1	to	·712
Philæmatomyia gurnei	1	to	·733
Philæmatomyia lineata	1	to	·777
Philæmatomyia insignis	1	to	1·411
Hæmatobia irritans	1	to	1·86
Stomoxys calcitrans	1	to	1·91
Lyperosia minuta	1	to	2·53
Glossina submorsitans	1	to	3·70

As will appear later, the progressive increase in the length of the haustellum is directly proportionate to the degree of fixation of the joint between the discal sclerite and the labial gutter, and to the degree to which the haustellum is drawn out to a point.

The *rostrum*, in addition to the reduction in size and the limitation of movement, is a much more firm and rigid structure than that of *Musca*; the

investment of the fulcrum in the membraneous wall is closer and the air sacs posterior to the fulcrum, by the distention of which the rostrum is pushed forward, are not nearly so conspicuous. The lateral plates of the fulcrum extend further forward, and the membrane uniting them on the anterior surface is thicker and merges indefinitely into the chitin at the sides. On the other hand, the anterior arch is not thickened into a stout bar for muscle attachment, and the whole structure is more closely fixed to the head than in the species previously considered.

The buccal cavity has undergone a remarkable transformation. Elongation is foreshadowed in the case of *Philæmatomyia insignis*; in the *Stomoxys* group we find that it has gone on to such an extent that the cavity has entirely lost its original shape and structure, and is converted into a duct with specialised walls, connecting the food canal in the haustellum with the pharynx. It is essential that this duct should be capable of flexion without occlusion of the lumen, for these flies feed with the joint between the haustellum and the rostrum a little flexed, and not with the whole proboscis fully extended as in *Musca*. When the organ is in the resting position the buccal cavity forms a tube at the lower end of the rostrum, the upper end of the tube being in line with the pharynx and the lower end with the haustellum, so that there is a point about its middle portion where it is flexed at a right angle. To ensure that flexion will not result in the occlusion of the lumen the wall of the tube is composed of two parts, an inner and outer; of these the inner consists of a simple tube of thin but rigid chitin in the upper half, where it is in line with the pharynx, and below this of a softer membrane. Outside this there is a series of transverse rings, thicker behind than in front, and approaching one another in the middle line behind so closely as to appear to be fused with one another. These rings will thus keep open the lumen of the tube should it be flexed during the act of feeding,* whereas the food channel of *Musca* is probably blocked in the flexed position by the approximation of its walls at the buccal cavity. In all the Muscid biting flies the buccal cavity is merely a channel, dilated in the early forms and tubular in the higher, which connects the food canal in the *haustellum* with the pharynx. It takes no part whatever in the sucking action.

The *haustellum*, instead of the loose cylindrical arrangement of chitin and membrane seen in *Musca*, is here a compact and almost entirely chitinous spindle, tapering gently from the expanded upper portion, known as the "bulb", to a point. The entire surface as seen externally is composed of the mentum

* This arrangement of chitinous rings has another and more important object, *viz.*, to prevent occlusion of the channel when a negative pressure is brought about in the pharynx, into which it opens, during the act of sucking.

The negative pressure in such a fly as *Stomoxys*, which fills itself to repletion within a few minutes, must be much greater than in the pharynx of intermittent feeders such as *Musca*.

of the labium, the lateral portions of which curve inwards and forwards so as to almost meet in front. The labial gutter lies out of sight between the edges of the mentum, and the membrane uniting the two is of very small extent. There are no large pigmented macrochætæ on the mentum, and the few hairs which are present are short and inconspicuous.

The *labella* have undergone a complete transformation from the type seen in *Musca*, and have become converted into a pair of small compact and partially fixed organs, the sole function of which is to pierce a hole in the skin of the host. In consequence of the loss of function the pseudo-tracheal membrane has disappeared, and it is only in *Hæmatobia*, the first member of the group, that traces of it can be recognised. The hæmatocœle, or space between the inner and outer walls of the labella, being no longer required to contain enough blood to distend the large oval lobes, has become very much reduced in size, and all that remains of the walls is sufficient to cover the teeth and the interdental armature in the position of rest. Both joints of the labella are consolidated; the anterior joint is limited in movement, but the posterior one permits of an even greater range of movement than in *Musca*.

The teeth are not, as one might expect, larger than those of *Philæmatomyia*, but the mechanism by which they are brought into play is a much more efficient one. All the teeth of one side are attached to one another by their bases, and the ridge of chitin so formed lies parallel with the edge of the discal sclerite, though it is not continuous with it. The interdental armature persists; it varies with the species in matters of detail, but is always attached to the prestomum in a manner similar to that in which the Y-shaped strands of chitin terminate in this region in *Musca*. Certain accessory structures, probably sensory, also become prominent.

The discal sclerite appears in a new form, which is not, at first sight, at all comparable with that of either *Musca* or *Philæmatomyia insignis*. Closer examination, however, reveals their essential similarity and homology. In all three flies it has the form of a funnel-shaped collar of chitin, surrounding the prestomum, and articulated with the ridge of chitin formed by the united bases of the teeth in front and with the labial gutter behind. The funnel is composed of two flattened plates, roughly oblong in shape, with the vertical diameter greater than the antero-posterior, and the distal border concave. They are continuous on the anterior borders with the median fissure between the labella, and are united ventrally. The space between them, which appears empty in sections, is oval in shape, and broader in the middle than at the upper and the lower angles. These flattened lateral portions represent the labellar rods. On the ventral side there is a third piece, always more conspicuous in sections than in cleared preparations, which binds the two lateral plates

together and forms the floor of the funnel. This represents the axial apophysis, a term which was first applied by Stephens and Newstead to this piece in *Stomoxys*, and subsequently used by me to indicate its homologue in *Philæmatomyia insignis.* The ridge of chitin at the bases of the teeth is closely apposed to the concave distal border of the sclerite, and is firmly bound down to it by a narrow band of fibrous tissue. The ridge is also attached by a fibrous band at the point where the lateral walls and the axial apophysis fuse together at the anterior ventral angle. The posterior end of the sclerite is irregular in shape, and articulates with the end of the labial gutter in a manner which differs slightly in the three forms, but in all cases is such as to indicate that the range of movement at this joint is a very small one, not in the least comparable to that in either *Musca* or *Philæmatomyia*, but more marked in *Hæmatobia* than in *Stomoxys.* The sclerite has, in fact, become fixed in the position of extension, as seen in *Philæmatomyia* when the labellar rods are in line with the labial gutter and the axial apophysis directed straight downwards. Normally the labella are directed a little backwards from the long axis of the labium, and are brought into line with it when the parts are in use, in the same way that the discal sclerite is erected in *Musca.*

As a consequence of this fixation of the anterior joint, the muscles which act upon it are reduced, together with the extent of their surface of origin. The anterior and median set of muscles is reduced to a very much smaller size than is found in *Philæmatomyia*, and the keel of the labial gutter from which it arises is diminished to a commensurate amount progressively in the three flies of the series. It is interesting to note that with the shortening of the arm of the lever to which this muscle is attached there is a corresponding decrease in the distance between its origin and insertion, for we find that the keel of the gutter, which in *Philæmatomyia* is attached to the upper portion only, is in these flies situated at the lower end, and that it becomes less extensive and more distal in position progressively with the other changes. The labial gutter itself, having no longer to bear the strain of a powerful pair of muscles, and since it is to a large extent replaced as a supporting structure by the mentum, reverts to its original function of protecting the labrum-epipharynx and hypopharnyx, and is composed of chitin little thicker than that of the mentum; the thickness, however, varies according to the amount of muscle attached to it, and is much greater in the region of the keel and at the extreme lower end, around the articulation, than further up. At the same time the distinction between the lateral and the median portions of the gutter remains well marked at the distal end, and they are here moulded so as to form a more or less complex joint with the discal sclerite.

The posterior articulation, between the fork of the mentum and the furca, now becomes the most important joint in the proboscis, and is specialised to a

high degree. In the case of *Philæmatomyia* both the joints probably come into play; the anterior one allows a backward rotation of the labellar rods on the end of the labial gutter, so that the teeth can sweep backwards across the skin, while the posterior one allows the teeth to be pulled outwards, traction being exercised on the inner walls of the labella by means of the intimate attachment of the furca to the outer wall. In this series of flies the first action is restricted to the straightening of the labella on the labium, and all the cutting is performed through the last joint, the various parts of which are modified and strengthened in accordance with their increased functional importance. The actual line of the joint has become displaced backwards, so as to lie between the furca and the proximal portion of the arm of the fork.

The posterior margin of the lower end of the mentum is not notched as in *Philæmatomyia*, but shows at most a shallow groove. On either side of this there is a thick rod of chitin, having the shape of an elongated wedge with its base directed distally and its most prominent angle turned outwards; this corresponds to the proximal division of the arm of the fork. The *furca* is reduced in size in accordance with the greatly reduced diameter of the labella; it is a wide and thick arch, the middle portion of which articulates with the thickened ends of the arms of the mental fork. On each side of it there is a short thick rod of chitin, closely pressed against the furca laterally, and having its proximal end only slightly separated from the fork of the mentum; this is the distal joint of the fork, which in *Philæmatomyia* lies parallel with the furca when the labellar rods are rotated into a position corresponding to that in which they have become fixed in the *Stomoxydinæ*.

The outer wall of the labella is almost entirely composed of a sheet of rather thin chitin, which is intimately connected with the extremity of the furca on each side. It reaches to the distal edge of the labella, and there bears a fringe of more or less conspicuous hairs, those of the two sides intermingling when the labella are closed. At the margin it gives place to a softer and more flexible membrane, which occupies the inner surface and bears the teeth and connected structures, and is continuous with the thicker fibrous tissue which unites the teeth to the discal sclerite. In this way the teeth are connected much more directly with the furca than in any of the flies previously considered.

The great increase in the strength and importance of this joint has brought about other changes in the structure and relations of the parts. Most important of these is the great increase in the size of the muscles which act on the posterior joint, and which are homologous with the posterior and lateral muscles, or retractors of the furca, in *Musca*. As the mentum is now narrowed to a point, the muscles are displaced to the upper end, which is dilated into the

"bulb" to accommodate them, and they are connected with their insertions by long tendons. The tendon of insertion is spread out after the manner of an aponeurosis. In addition to its main insertion into the lateral arm of the furca, it sends numerous fibres to the external wall of the labellum, and to the distal portion of the fork of the mentum, which is displaced forwards and fused with the labellar wall as stated above.

The mechanism of the proboscis has been dealt with in the description of *Lyperosia*, and the other species show no divergence from that fly except in very minor details. It will be evident from that account, bearing in mind what occurs in *Musca* and in *Philæmatomyia*, that the efficiency of the cutting action depends entirely on the great increase in the strength of the posterior articulation between the labium and the labella, and in the muscles which act upon it. The anterior joint is on the contrary limited to such movement as will place the teeth in the position for the next cut, and the muscles which act upon it, not having to work against the same resistance, are of much smaller size. A further point which is of some importance in considering the mechanism both of these flies and of *Glossina* is that there is a membraneous interval on the lateral aspect of the haustellum in the neighbourhood of the joints, which, while it permits of free backward rotation of the furca, would also detract from the rigidity of the proboscis as a whole, were it not for the fact that the labial gutter reaches its greatest thickness at this point.

The labrum-epipharynx and the hypopharynx are remarkably little altered from the *Musca* type. As a consequence of the narrowness of the groove in which they lie, they are narrower than those of the non-biting flies, and as from the same circumstance they are much better protected, they are more slender and less rigid. The labral apodemes are also somewhat shorter, corresponding with the reduction in size of the rostrum as a whole, and are not quite so thick. The most important feature of the food canal is that the fusion of the two lips of the groove in the epipharynx takes place at a higher level in these flies than in *Philæmatomyia*, which shows that there is a tendency for it to become converted into a closed tube, a continuation into the proboscis of the stomadeaum as a closed canal, instead of as dorsal and ventral outgrowths. On the other hand, the separation of the lower lamina of the hypopharynx from the labial gutter is maintained as in other blood-sucking flies.

Hæmatobia (Plate III).

The proboscis of *Hæmatobia* presents a most interesting feature in the possession of the remains of a pseudotracheal membrane, and certain other peculiarities which indicate that it represents a relatively early stage in the

evolution of the blood-sucking proboscis. I am indebted to Captain Patton of this Institute for named specimens of *Hæmatobia irritans* and to Mr. Howlett for specimens sent from Pusa. Unfortunately the genus does not appear to occur in this neighbourhood and lack of fresh material renders my description somewhat more meagre than it would otherwise have been.

The relative lengths of the rostrum and the haustellum are practically the same as those in *Stomoxys*, but the difference in shape is greater than the measurements indicate, for the thickest part of the labium is at the junction of the upper and adjacent fourth, from which the proboscis narrows evenly to the furca, while in *Stomoxys* the greatest thickness is well above this line, and distal fourth of the labium is practically of a uniform diameter.

In the position of rest the labella are bent distinctly downwards on the end of the labium, much more so than is the case in *Lyperosia* or *Stomoxys*, and are distinctly wider than the adjacent part of the labium; they also bear a fringe of moderately large macrochætæ along the distal margin. All these points indicate a closer relationship with the *Musca* type. The keel of the labial gutter, though not so thickly chitinised as that of *Philæmatomyia*, is almost of equal extent, and is present in the upper two-thirds of the labium, reaching in the upper part almost to the mentum; it thus provides a considerable area for the attachment of the anterior set of muscles. The gutter itself is strong and deeply pigmented, and at its lower end (Plate V, figure 25) the separation between the lateral and the median portion is well marked. The articulation between it and the discal sclerite is obviously one which allows of a greater range of movement than can take place in *Lyperosia*. The lateral portions of the labial gutter are produced into rounded processes, which are inclined slightly backwards (downwards in the position of rest, the labium being horizontal) and extend beyond the median portion of the gutter. They lie in an L-shaped depression at the upper and anterior angle of the sclerite, and are in contact with it when the labella are straightened on the labium, but separated from it when the labella are in the position of rest. The bottom of the median groove in the gutter is produced beyond the rest of the median portion and fits into the space between the lateral walls of the sclerite, through which it can be seen in well cleared preparations. The labella, through the discal sclerite, can therefore be straightened on the labium, and maintained in the extended position by the pressure of the upper border of the lateral wall of the sclerite against the lateral portion of the labial gutter. When in this position the median portion of the gutter projects between the two walls of the discal sclerite, and will afford additional support. The discal sclerite itself presents no differences from that of *Stomoxys*, except that the axial apophysis is more pear-shaped, and that its pointed end projects further forward.

The outer wall of the labellum is partly membraneous and partly chitinous. The chitinous portion is in the form of a plate shaped like a cockle-shell; the rounded edge of this forms the lower border of the labellum, and bears some of the hairs forming the terminal fringe; the upper end, which corresponds to the hinge of the shell, is thickened and drawn out, and is closely fused with the extremity of the furca. The upper portion of the posterior side of this plate is also attached to the lower border of the furca by a thin chitinous prolongation, so that the whole outer wall of the labellum is firmly bound down to it, and must follow it when it is drawn upwards. This plate corresponds in position to the space on the inner wall occupied by the teeth, which can be seen by focussing through it in a cleared preparation.

The rest of the outer wall is membraneous, and is continuous with a membraneous area, on the anterior and lateral aspects of the end of the labium, which extends upwards above the furca for a distance equal to the length of the labella. The membrane is quite different in appearance to any that is met with in the flies already described; it consists of a transparent, homogeneous, and structureless groundwork, in which there are placed small plates of thin chitin, irregularly oval in shape and set close together, though not actually touching one another. At its boundaries it merges indefinitely with the attenuated edges of the chitinous plates, and at the border of the labella it is continuous with the inner wall.

At the distal border of the labella there is on each side a row of five finger-like flaps, passing distally beyond the margin, and continuous with its outer wall. They are processes of the labella, and it is on their inner surfaces that the channels of the pseudotracheal membrane are to be found; they will be dealt with in connection with the structures found on the inner wall of the labella.

The teeth are five in number on each side. Counting from the dorsal or anterior side, the second is the largest, the first and third equal in size and slightly less than the first, and the third and fifth distinctly smaller, the fifth being the smallest of the set. The largest tooth is about one-fourth the length of the labellum. Each tooth is conical in shape and about twice as long as it is broad; the distal end is produced to a blunt and slightly curved point, just below which there is a notch in the margin of the tooth, the edge proximal to the notch forming a second cutting point. The notch is situated on the dorsal borders of the first and the second teeth, on the internal border of the third, and on the posterior or ventral borders of the fourth and fifth. On the internal surface of each tooth, that is to say, on that surface which is turned outwards when the teeth are everted, there are a number of peculiar secondary teeth (Plate III, figures 18 and 19). These are situated about the middle of

the surface, and are arranged in rows across the tooth. Each is a small oblong or oval eminence, the distal end of which is free from the surface of the large tooth and forms a cutting point. All the teeth are united at their bases by chitinous prolongations, the union of the first two and the last three to one another being the most firm. When flattened out by the pressure of the coverslip, as in the preparation drawn (Plate IV, figure 22), the bases of the teeth are in the same straight line, but when the proboscis is mounted whole it is seen that in the position of rest they are arranged in a curve which corresponds with the line of the distal margin of the discal sclerite.

The interdental armature consists of a series of lanceolate leaf-like blades closely resembling the "petiolated blades" described by Stephens and Newstead. Like those of *Stomoxys*, they are extremely delicate objects, containing little or no pigment. Their surface is finely granular, and the stalks from which they arise are thicker and flatter than those of *Stomoxys*. They are arranged as follows:—There are three sets, similar to one another, between the first and second, second and third, and third and fourth teeth. Each of these consists of a central stalk, from each side of which three blades arise and pass forwards, those of the two sides diverging from one another. The terminal pair of blades lie on either side of the pseudotracheal channel. External to the first tooth there is a set of smaller and narrower blades, five pairs on a common stalk, the terminal blades also surrounding the termination of a channel. External to these there are two stouter elongate filaments of chitin arising at the base of the first tooth. Between the fourth and fifth teeth there is a common stalk bearing only two pairs of smaller blades, the diameter of which is little greater than that of the stalk. External to the fifth tooth there is another stout stalk which bears two pairs of blades, and arises from the ridge of chitin at the base of the tooth. On account of the extremely heavy pigmentation of the teeth and their close approximation I have not been able to ascertain whether the middle sets of blades arise from the teeth or from the membrane of the inner wall of the labellum.

Between the petiolated blades, and situated opposite the apices of the teeth, there are certain prominent hairs, the position of which should be noted. These correspond to those termed by Stephens and Newstead the "rod-like" hairs; they are short and stout, arise from prominent raised and expanded bases, and terminate in truncated ends. They are darkly pigmented and conspicuous, slightly curved, and about five or six times as long as thick. The appearance of a groove is probably due to the presence of a central canal and not to an actual groove. They are arranged as follows:—One opposite the first tooth, two opposite each of the second, third, and fourth teeth, and one opposite the fifth tooth; in addition, there are two smaller ones placed between the small

petiolated blades external to the first tooth and the extreme anterior strand of chitin. These rod-like hairs occur in all the biting flies dealt with in this paper, except the first two species of *Philæmatomyia*, and presumably have some special sensory function connected with the biting habit.

The membrane forming the inner wall of the labellum, as far forward as the attachment of the two distal petiolated blades to the common stalk, is transparent, homogeneous, and apparently structureless; its existence is only shown, in cleared preparations, by the way it holds the parts together. But distal to this it consists of a membrane of the same nature as that which forms the non-chitinised parts of the external wall, and is produced beyond the distal border of the labella as the inner wall of the finger-like flaps already referred to. The structure of these flaps is as follows:—

Each flap is roughly triangular in shape, and consists of two walls, an inner and an outer. The outer wall is continuous with, and of the same structure as, the membrane which forms part of the external wall of the labellum, and which dips in between the two lobes at the anterior median fissure. The squamæ in this region are thinner and less sharply defined than elsewhere, and are all more or less pointed and distally directed. Those at the extreme tip of the flap are turned inwards towards those of the opposite side. In the middle line of each flap there is an area over which they are deficient, corresponding in position and extent to the pseudotracheal channel on the inner wall. The inner wall of each flap is continuous with the homogeneous and structureless layer of tissue which lies subjacent to the teeth, the line of junction between the two being situated at the level of the distal border of the chitinous plate in the external wall of the labellum. The distal portion, that is to say, that which is opposite to the outer wall of the flap, is composed of a membrane similar to that of the outer wall, but the squamæ are here so disposed as to form a shallow channel, the representative of the pseudotrachea. The plates are only found in the area which corresponds to that on the outer wall in which they are absent, so that the distinction between the two layers of the flap can only be made out by careful focussing in a preparation which has not been compressed by the coverslip, and by using a high magnification. The channel is formed by a series of thin transversely elongated plates, set side by side and fitted loosely to one another; each plate is curved to such an extent that the channel, in cross-section, would be approximately semi-circular, and the lateral extremities of the plates are alternately bifid and narrowed. At the distal end the channel is turned upon itself in such a way that the last three or four of the plates are in the same line as those proximal to them, or nearly so. Opposite to the termination, which is not at the distal end of the flap, but some distance away from it on account of the bend at the

end of the channel, there is a minute, short and stout hair set on a thicker base.

At the proximal end of the flap the flat plates which form the groove are replaced by rounder rods very similar in appearance to those of ordinary pseudotracheal channels. The transformation takes place gradually and regularly, and there is no doubt that the plates in the region of the flap and the rings between the petiolated blades are the same structure in different forms. The termination of the pseudotracheal channels in the region of the teeth is abrupt and simple, and there are no T-shaped rings, or rings split in half, such as have been described in the previous forms. The terminal rings differ from the rest only in being produced into U-shaped loops.

There is no doubt that this structure represents a pseudotracheal membrane, and is homologous with that found in *Musca*. In order to ascertain definitely to what degree the function is retained it would be necessary to examine fresh specimens, but it appears likely that the channels do actually act in conveying the fluid to the prestomum. The space between the two walls of the flap is evidently a part of the hæmatocœle, and will therefore be distended by the blood of the fly as in *Musca*. It was shown in the case of *Lyperosia* that the teeth are returned into position for cutting by the distension of the hæmatocœle. In the case of *Hæmatobia* this distension will also result in the approximation of the two ends of the elongated transverse plates, in the same manner as that in which the pseudotracheal channels are closed in *Musca*. Possibly the two ends interlock, leaving only the interbifid spaces open as in the non-biting Muscids.

The occurrence of this structure in a fly with a piercing proboscis is very remarkable, and has an especial interest as indicating the source of the pseudotracheal channels. Evidently these, in *Musca* and its allies, are mere thickenings of the wall of the labella, and are similar in origin to the squamæ in *Stomoxys* and *Hæmatobia*.

Stomoxys.

The anatomy of the proboscis of *Stomoxys* has been described in great detail by Stephens and Newstead, and I may say at once that as regards the details of structure and armature there is little to add to their account, my dissections having in the main confirmed their results. Their work on *Stomoxys*, however, was done after an examination of *Glossina*, the most complex and highly specialised of the series, and the true homology of the parts, which can only be understood by proceeding from the simplest forms to the more complex, is not brought out in their paper. The terms used by them are descriptive and

provisional only, the establishment of a definite nomenclature having been postponed pending further research. The account therefore lacks cohesion, and is difficult to follow unless one has the actual preparations before one. It will therefore be necessary to explain the relation of the terms used by them to those used in this paper. In so far as they are applicable to structures not already named in *Musca*, their terminology has been retained and used in the previous papers of this series.

To commence with the labium: the whole of the chitinous wall as seen externally, including the bulb, I regard as the mentum, homologous with that of *Musca;* the two joints of the fork at the lower end are separated from one another, the proximal one being the support of the furca on each side, and the distal one pressed forward against the furca. The former of these is called the "ventral sclerite," the latter the "lateral sclerite of the fork." For the labial gutter and the keel I have used their terms, which are equally applicable to the corresponding parts in other flies. In the labial gutter they distinguish the lateral borders of the terminal portion concerned in the articulation as the "dorsal hooked sclerite" and the base as a separate sclerite, which unites with the lateral ones proximal to the articulation. In their description of the labella there is a good deal of confusion, owing partly to their having placed too much reliance on the appearances seen in sections, and to their not having recognised the nature of the joint. Their figures are so accurate and clear that the confusion of the text is to a large extent removed when one compares them with dissections. Their tooth plate (*k*) corresponds to that part of the sclerite which I have termed the labellar rod; the axial apophysis, as before, represents the tip of the discal sclerite which has become displaced upwards. The petiolated blades constitute the interdental armature; the "fork" is the furca, and should not be confused with the fork of the lower end of the labium. The tendon which is shown in their sections is the tendon of the muscle of the bulb, which pulls the teeth outwards and actuates the cutting mechanism.

With regard to the mechanism of the cutting apparatus my view, as explained in connection with *Lyperosia*, differs from theirs. I can find no joint in the whole of the proboscis which could permit of a lateral rotatory movement of the teeth, and the transverse muscles at the lower end of the labium fulfil a function entirely different to the one suggested by them. So far as one can gather from their paper these authors do not appear to have had access to fresh material for dissection, a most serious handicap, for without that, and a considerable quantity of it, it is extremely difficult to make sure of points such as these. The action of the muscles of the bulb can only be fully realised by dissecting out the bulk of the muscle and making traction on it while holding the labium firm at a lower point on the other side, thus imitating the natural

contraction of the muscle. This is a difficult manœuvre, and one requires a large number of fresh specimens to demonstrate the effect beyond doubt.

The proboscis of *Stomoxys* conforms to the general description already given; all the points which indicate an advance in specialisation are more marked in this fly than in *Hæmatobia.* The labium is more pointed, the bulb confined more to the upper part, and there are fewer and smaller hairs at the discal fringe and at the sides of the mentum, points which indicate that the organ is more adapted for piercing. As showing the greater fixation of the anterior joint, the labial gutter is not so well marked and its keel is confined to the distal part of the labium; the labella are not so large as those of *Hæmatobia* and are placed more nearly in the same long axis as the labium in the position of rest. The joint between the end of the labial gutter and the distal sclerite is a closer one, and the two parts are united by a strand of chitin which passes between the distal ends of the lateral portions of the gutter and the dorsal part of the sclerite, thus limiting still further the amount of movement between the two, already small by reason of the nature of the joint. The teeth and the other structures on the inner wall of the labella, which have been described in great detail by Stephens and Newstead, resemble generally the arrangement in *Hæmatobia,* but some structures described by these authors have not been recognised either in *Hæmatobia* or in *Lyperosia.* The external wall of the labella is much less chitinised, and the membraneous portion between the truncated end of the mentum and the furca is more extensive, and is marked by folds indicating its disposition when the furca is drawn upwards.

Lyperosia.

While one can readily believe that *Stomoxys* has had for its immediate ancestor a *Hæmatobia*-like form, it is clear that *Lyperosia* is not descended from the *Stomoxys* stem, but from a common ancestor of the two, although the relation between the three flies is a very close one. Perhaps when the opportunity occurs to examine some of the other genera of Muscid biting flies forms will be found which will explain more clearly the positions which these flies ought to occupy in the group.

In the greater length of the haustellum in proportion to that of the rostrum, and in the much more typical spindle shape of the labium, we have clear indications that this fly is more perfectly adapted for piercing the skin than is *Stomoxys.* But in other details, small in themselves but significant when taken together, the adaptation appears less perfect. The palps approximate more to those of *Hæmatobia* than to those of *Stomoxys,* a point on which systematists lay some stress. The distal border of the

labella has a fringe of macrochætæ which are distinctly more prominent than those of *Stomoxys,* though not so conspicuous as those of *Hæmatobia.* The external walls of the labella are far more chitinised than those of *Stomoxys,* though the chitin is thin and the plate which it forms is interrupted by the presence of longitudinal fissures, which will to a certain extent compensate for the rigidity. The form of the discal sclerite, however, shows clearly that *Lyperosia* is not directly related to either *Hæmatobia* or *Stomoxys,* and at the same time suggests that it is more specialised than either. In its general shape and relations it conforms to the type already described, but, when seen in section, it is found to be a much more complex structure, the relation of which to the mechanism of the joint it is by no means easy to determine. The change is limited to the axial apophysis, which has lost the solidity of the corresponding part in the other flies, and consists of a shell of chitin with cellular tissue inside. The proximal end is turned upwards behind the end of the labial gutter in a curious manner, and appears to take some part in the mechanism of the joint, though neither muscle nor tendon can be found attached to it. The joint between the labial gutter and the discal sclerite is of the most complex description, and can obviously permit of only a slight degree of movement.

Glossina.

Glossina is as widely separated from the flies previously considered as regards the structure of the mouth parts as it is in its other anatomical features and in its life history, and there is at least as wide a difference between its proboscis and that of *Lyperosia* as there is between *Lyperosia* and *Musca* in this respect. Nevertheless we find that the great changes in the anatomy of the parts are but an extreme instance of the adaptation of the Muscid proboscis to a blood-sucking habit, and there is little doubt that the proboscis of this fly is but a modification evolved from the *Musca* type.

The anatomy of the proboscis has been minutely described by Stephens and Newstead, but these authors have not touched on the subject from the point of view of this paper, and have simply described the appearances as seen, with a suggestion regarding the mechanism. My remarks on this fly will resolve themselves into an interpretation of the homology of the parts as described by them, and to a consideration of the mechanism of the proboscis as a whole, dealing in more detail, however, with the structure of the rostrum, which is not touched on in their work. My material has been limited to some dried specimens of *Glossina sub-morsitans,* for which I am indebted to Professor Newstead, and one specimen of *Glossina palpalis,* placed at my disposal by

Captain Patton. To make the most of such limited material the specimens, after clearing in potash, each for a different period, were mounted whole in different positions, and after examination replaced in clove oil, dissected, and remounted in balsaam. I have found no differences from the description or figures in either *palpalis* or *sub-morsitans*.

The proportionate lengths of the rostrum and the haustellum as given on page 45 are somewhat misleading, as the position in which the proboscis is held is a much more definitely fixed one than in the other flies, and it is not possible in cleared preparations to stretch the two divisions out into the same straight line. In the figures given by Stephens and Newstead and by Hansen, the haustellum is shown to be about three and a half times as long as the rostrum. The rostrum is short and compact, and is almost entirely occupied by the fulcrum, the space available for air sacs between its posterior plate and the limiting membrane being very small. The fulcrum is much more regular in shape and more evenly chitinised than in any of the previous flies. Seen in profile it has the shape of a triangle with three approximately equal sides; the posterior side is gently convex backwards, the anterior convex forwards in the upper part, where it is produced into a sharp angle, and concave below; the upper side is concave, but is not produced in the definite cornua at the posterior angle as in *Stomoxys*. The walls of the fulcrum are equally chitinised throughout, and from this fact and from the absence of ridges for muscle attachment, and from the lack of cornua at the upper aud posterior angle, one would infer that the movements of the rostrum on the head, though of the same nature as those of the other flies, are reduced to a minimum; and that the adaptation of the position of the proboscis for feeding is carried out by movements of the body of the fly and by the joint between the rostrum and the haustellum. The chitin of the anterior arch occupies a much larger proportion of the anterior surface of the rostrum than is the case in the other forms.

The *buccal cavity* approaches more to the type seen in *Musca* than to that of the *Stomoxys* group. It consists of a small chamber with chitinous posterior and lateral walls, formed from a small transverse plate, the up-turned sides of which are united anteriorly by a membrane. I am not able to say whether it has a dilator muscle or not. It is connected with the epipharynx in the same way as in *Musca*. The membrane which unites the buccal cavity with the pharynx is a very short one, and from the structure of this part of the proboscis it is evident that there is a little movement at the joint.

The briefest examination of the haustellum shows that the whole of it has become transformed into a piercing organ, and that the separation of the labella from the labium, though clearly marked, has not the same significance as it has in the *Stomoxys* group. All the structures have become most profoundly

modified, the armature has become a most complex one, and the nature of the joints has altered so completely that it is difficult to say in some cases exactly what they represent or at which point the movement takes place. The fundamental changes on which the appearance of the proboscis depends are the predominence of the labial gutter over the mentum in the narrow part of the proboscis; the fusion of the discal sclerite with the end of the labial gutter, resulting in the total disappearance of the anterior joint; and the conversion of a part of the outer surface of the labella, and a part of the surface of the labium itself, into a cutting apparatus. All this is but an extreme stage of what one sees going on in the evolution of the other flies.

To take these changes in detail: The bulb of the proboscis is evidently the same as that of *Stomoxys*, and may at once be termed a part of the mentum. But at the distal end of the bulb the thick and pigmented chitin of which it is composed gives place to a very much thinner sheet which is flexible and membraneous, and which cannot contribute to the rigidity of the organ. In the middle line it is provided with a bilateral row of peculiar spines, which extend right to the commencement of the bulb. (S. & N., figure 2, i, ii) Sections at any point between the labella and the bulb show that the wall of the mentum is a very thin one; on the other hand, the labial gutter is very well developed, and it undoubtedly constitutes the main support of the proboscis, thus reversing the conditions found in *Musca*. The membrane which unites the two is short, but in the sections figured it is shown as thrown into irregular folds, which are very noticeable in my preparations. They run obliquely upwards and inwards, not in the same way in all the preparations but varying in different positions of the labella, in such a way as to indicate that the labial gutter and the mentum do not always occupy the same position in relation to one another. The only trace of the keel of the gutter that is to be found is a thin slip of chitin extending less than half the distance between the gutter and the mentum in the bulb. In the middle line between the two lateral halves of the gutter there is a deep pocket-like indentation in which the hypopharynx lies.

The posterior joint, between the labium and the labella, has undergone most profound changes, and it is no longer possible to recognise the constituent parts as seen in *Stomoxys*. But by reverting to the appearance in *Musca*, and to the essential nature of the parts, one is able to trace the homology fairly closely. The furca in *Musca* is nothing more than a thickening of the external wall of the labella on each side; in the biting flies allied closely to *Musca* it becomes transformed into a strong bar because the important muscles of the bulb are inserted into its lateral arms. In *Glossina* we find a reversion to the more primitive type. The muscles of the bulb are apparently not inserted

by one thick tendon, but are spread out over a considerable area of the external wall, and the necessity for a thick rod therefore does not exist. There is instead a transverse plate, which is united with a longitudinal one.* The latter may, without any great stretch of the imagination, be recognised as formed by the fusion of the two rods which form the fork of the mentum, the ventral sclerites of Stephens and Newstead. These authors have pointed out that the lateral arms of this T-shaped piece are variable in position according to the degree of eversion of the labella, exactly as one would expect if they represent the arms of the furca. A considerable amount of the muscle of the bulb is probably inserted into the region referred to as the "dark ventral chitinous area."

The anterior joint has disappeared, and if the sections are traced downwards it will be seen that the walls of the labial gutter become directly continuous with the inner walls of the labella, just as the outer walls of the mentum are continuous with their outer walls. There is, however, a thicker portion shown in their figures 15 to 19, which corresponds to the position of the discal sclerite; the hypopharynx lies at the upper end of this thickening in the position of rest. The situation of the thickening of the internal walls corresponds in position to that of the "dark area" on the outer walls.

The interpretation of the mechanism of the cutting apparatus offers no difficulties. The teeth resemble in shape, though not in arrangement, those of the preceding examples, and the "fans" distal to them are evidently the homologues of the petiolated blades of *Stomoxys*, and therefore of the pseudotracheal rings of *Musca*. The teeth are united at their bases by the three pieces of chitin which bear the rasps, in a manner corresponding generally with that in which the teeth of *Stomoxys* are attached to the tooth plate; whether the rasps really represent the united bases of the teeth or are a detached part of the discal sclerite it is not possible to say. The "jointed chitinous rods" appear to be the rod-like hairs, which, in order to maintain their position in advance of the teeth during the act of cutting, have passed through the wall of the labellum in the manner described.

The mechanism of the proboscis is evidently the same as that of the *Stomoxys* group. But here there is an important point which should be noted in the interpretation of the drawings. I pointed out in connection with *Lyperosia* that the appearance of the labella in the everted position in cleared preparations is not the same as that in fresh dissections, for, when the muscles are dissolved by the action of the potash, the parts relax; it is impossible to get cleared preparations which show the true position of the teeth during the

* An examination of more material has convinced me that the longitudinal and transverse portions of this T-shaped rod are not continuous with one another, but are united by a narrow strip of membrane. This serves to hinge them together, while permitting of free movement.

act of cutting. The same applies to *Glossina*, and I have not the least doubt that the lateral arms of the " fork " are turned much further backwards, and the teeth much more fully everted, than is shown in figure 8 (S. and N.). The chitin between the " dark area " and the bases of the rasps is evidently thin and membraneous, and it is here that the eversion takes place when the teeth are brought into action.

There is a membraneous area between the end of the labial gutter and the fork, as is found in the other flies. But in the case of *Glossina*, the entire mentum, with the exception of the bulb, is drawn upwards when the teeth are everted, and the membrane between it and the labial gutter is thrown into the folds already mentioned. The posterior surface of the mentum is armed with spines which would appear to have some cutting action, and it is probable that many of the spine and tubercles so minutely described are really cutting organs accessory to the teeth and rasps, and that not only the inner wall of the labellum, but its outer wall and the outer wall of the labium also are a part of the cutting apparatus. The whole is actuated in the same way as in *Stomoxys*, by the contraction of the muscles of the bulb, the long tendons of which are so conspicuous in the sections. But instead of a simple eversion of the teeth the whole of the inner wall of the labellum, its outer wall, and part of the mentum are drawn up, until the thickened part which represents the discal sclerite is at the tip of the proboscis. When this has occurred the labrum-epipharynx and the hypopharynx are at the point of puncture, and are able to draw in the blood. The disproportion between the length of these two organs and the total length of the labium and the labella is less than that seen in *Stomoxys*, and this corresponds with the shorter space between the tip and the softer portion of the inner wall at which the eversion takes place. The short excursion of the cutting surface is more than compensated for by its greater lateral extent, for the armature extends from the rasps to the bulb, and includes portions of the inner and outer walls of the labella and also of the posterior surface of the mentum.

The labrum-epipharynx and the hypopharyx are altered in such a manner as one would expect. On account of the more pronounced stylet-shape of the haustellum as a whole, they are reduced in diameter and fit much more closely into the groove in the labial gutter. They are more firmly united to one another, so as to constitute almost a closed tube, and the labrum is closely fitted to the labium by means of an elaborate arrangement of interlocking teeth. Between the labrum and the epipharynx a small comma-shaped interval can be seen in the region of the bulb, in the situation in which the fan-shaped muscle is found in *Musca*. Stephens and Newstead state that the labrum, by which term they designate the combined organ, fuses at the upper end with

the bulb, but they do not describe how the separation between the labral and epipharyngeal portions of the organ occurs, and I have been unable to determine this point for want of series of sections. It is a little unlikely that labrum and labium would unite directly. From the fact that the section shown in their figure 25 includes the attachment of the palp, one would suppose that the section is an oblique one, through the lower end of the rostrum, in which case the anterior membraneous portion is really the anterior wall of the rostrum. It is, as a matter of fact, extremely difficult to get the rostrum and haustellum sufficiently into line with one another to get a series of transverse section of both, as I found in the case of *Lyperosia*. It would be still more difficult to do it with *Glossina*, in which the angle is a much more permanent one.

I have never myself seen *Glossina* in the act of feeding, nor is the opportunity likely to occur. I have selected from the numerous descriptions of its mode of feeding one by an observer who presumably had no expert knowledge of the subject, and merely recorded what he saw. It accords so well with what I believe to be the mechanism of the proboscis that I cannot forbear from quoting.

Captain Crawshaw writes as follows in 1896: "When a 'Tse-tse' settles "with the intention of feeding...........he inserts his proboscis, lowers his head, "and raises his abdomen till it is almost vertical; when doing this and for some "time after he has commenced sucking, he works his wings, buzzing in a minor "key, rather like a bee when held forcibly, though not so powerfully; when the "keenness of his appetite has been somewhat appeased, he stops working his "wings and sucks in silence. If left to himself he will suck until................" The raising of the abdomen is rendered necessary in *Glossina* by the fixation of the joint between the rostrum and the head. It does not occur in *Stomoxys*. The period during which the fly produces the buzzing sound is that in which the wound is being made and the proboscis thrust into the skin, and while this is going on the fly is not absorbing food. The motion of the wings and the buzzing sound are produced by the excessively rapid respiratory movements which distend the hæmatocœle with blood; this must occur after each contraction of the muscles of the bulb, in order that the teeth may be replaced in position for the next cut, as explained in connection with *Lyperosia*. I have never distinguished any sound produced by *Stomoxys* while inserting its proboscis, but a faint vibration of the wings can be seen. The eversion and replacement of the cutting teeth in *Glossina* must of course occur with very great rapidity. As I have noted elsewhere, the cutting apparatus of the Diptera is a good example of the extraordinary rapidity of action of which insect muscle is capable. It is possible that by ascertaining the exact pitch of

the note one could fix definitely the number of contractions made per second by the muscles of the bulb, for there will of course be one contraction for each respiratory movement, and it is these respiratory movements which produce the vibration in the wing.

When the wound has been made to a convenient depth the buzzing ceases, the labella are held in a permanently everted position, and in a very short time the fly sucks up enough blood to distend the abdomen. The motion of the wings does not cease, as Captain Crawshaw supposed, when the appetite is appeased, but at the moment the fly commences to suck, and is no longer occupied in making the wound. The length of the narrow part of the proboscis, the extremely efficient nature of the biting parts, and the rapidity with which the abdomen distends with blood, make it probable that the fly gets well below the epidermis and into a vascular layer before commencing to suck.

In several other accounts it is stated that the bite of *Glossina* causes pain, not at the moment the fly settles down, but after a short interval. One interprets this, as in the case of the mosquito bite, as due to the fact that it is the saliva injected into the wound which causes the pain, and not the actual making of the wound. The cutting parts of *Glossina* are so small and so sharp that one would not expect them to cause pain.

Summary and Conclusions.

1. The blood-sucking Muscidæ are descended from a Musca-like ancestor. The entomological facts make it improbable that the flagellates found in the alimentary tract of blood-sucking flies, and of non-blood suckers which are allied to them, are derived from the parasites in vertebrate blood. They are probably the descendants of parasites which entered the alimentary tract at the time the ancestors of the flies were mandibulate and omnivorous.

2. The first steps in the evolution of the blood-sucking habit can be seen at the present day in those flies which are blood-suckers but have no biting mouth parts. These depend on true biting flies for the making of the wound.

3. In the genus *Philæmatomyia* there are three species which show separate steps in the modification of the Musca-like proboscis to a biting apparatus. The changes all depend on the increase in size and functional importance of the prestomal teeth. They are :—Increase in the strength of the discal sclerite ; separation of the axial apophysis and labellar rods, and displacement upwards of the former ; approximation of the bases of the teeth and the separation of their bases from the discal sclerite, to allow of greater freedom of movement ; displacement of the teeth to the distal end of the labellar rods ; consolidation of the anterior joint between the labial gutter and the discal sclerite ; great increase in the strength of the labial gutter and the development of a " keel " to provide additional attachment for the muscles ; some consolidation of the posterior joint with a thickening of the furca ; increase in all the muscles ; some diminution in extent of the pseudotracheal membrane and the development of the interdental armature from the rings of the pseudotracheæ.

4. Between the genus *Philæmatomyia* and the *Stomoxydinæ* there is a wide gap. Future research will probably reveal other forms intermediate between these.

5. In the *Stomoxydinæ* the proboscis is a piercing one in the true sense of the word. Its spindle shape is due to the increase in extent and alteration in shape of the mentum as seen in *Musca*, and to the diminution in the size of the labella. The biting apparatus is altered upon the following lines :—The teeth are reduced in number and in size ; the interdental armature, which takes on the filtering function of its homologue, is highly developed ; the discal sclerite is altered to a funnel-shaped piece ; the articulation between the discal sclerite and the labellar rods is more or less fixed in the position of extension ; the posterior joint becomes of great importance, and the furca and the arms of the fork of the mentum are both greatly increased in thickness and reduced in size ; notwithstanding the chitinisation of the rest of the wall of the haustellum, there is

a membraneous interval left in the region of the joint which permits the furca to be rotated freely backwards.

6. In all the flies dealt with, in the order given, there is an increase in the relative length of the haustellum, and a diminution in that of the rostrum, together with some diminution in the amount of movement between the latter and the head capsule.

7. *Glossina* represents an extreme case, and there is a wide interval between it and the *Stomoxydinæ*. The alterations in the shape and the diminution in the amount of movement are the same in kind as in *Stomoxys*, but in greater degree. The teeth are more complex, and the interdental armatures are represented by the "fans." The cutting apparatus is not limited to the inner wall of the labellum, but extends on to the outer wall as well, and when the muscles of the bulb contract the outer wall is pulled bodily upward as the inner wall is everted. The discal sclerite is fused with the end of the labial gutter and cannot be recognised as a separate sclerite. The furca and the two arms of the fork of the mentum are closely approximated to one another. The main support of the narrow piercing part of the proboscis is the labial gutter, which is very strong, while the mentum in this region is semi-membraneous. The rostrum is capable of so little movement on the head that the fly has to raise itself on its hind legs to bring the proboscis into position for piercing.

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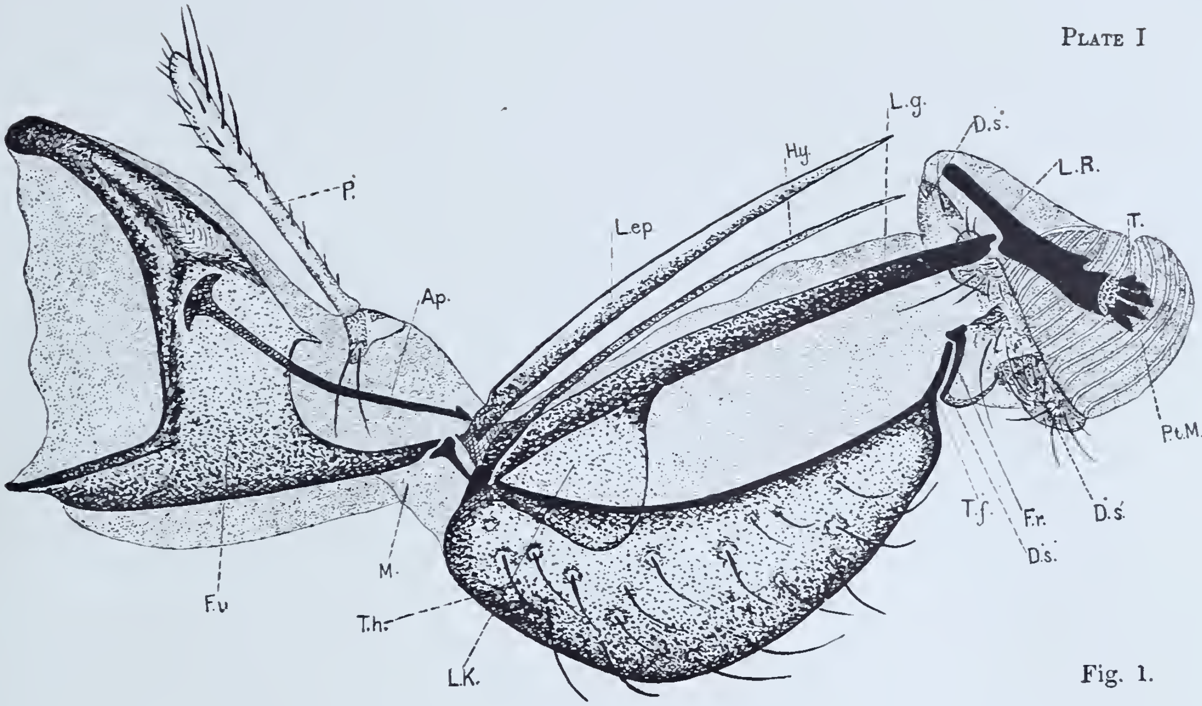
PLATE I.

Figure 1.—The proboscis of *Philaematomyia insignis*, Austen, from a cleared preparation p., the palp. ap., the apodeme. fu,, the fulcrm. m., the membrane of the wall of the rostrum. L.ep., the labrum-epipharynx. Hy., the hypopharynx, L.g., the labial gutter. Th., the memtum (theca). L.K., keel of the labial gutter. L.R., the labellar rod. T., the teeth. Pt. M., the pseudotracheal membrane. T.f., fork of the mentum, Fr., the furca. D.S., chitinous plates in the outer wall of the labella, reflexed × 33.

Figure 2.—The proboscis of *Lyperosia minua*, Bezzi, from a cleared preparation. f., the posterior cornu of the fulcrum. f'., the anterior arch of the fulcrum. f''., the funnelshaped distal end of the fulcrum. s.d., the salivary duct. ap., the apodeme. b.c., the buccal cavity. tr., trachea. l.g., the labial gutter. mt., the mentum. b., the bulb, l.g., the labial gutter. m. a., the membraneous area which allows of rotation backwards of the furca. v.sc., ventral sclerites (the proximal portion of the fork of the mentum). fu., furca. lb., the labella × 160.



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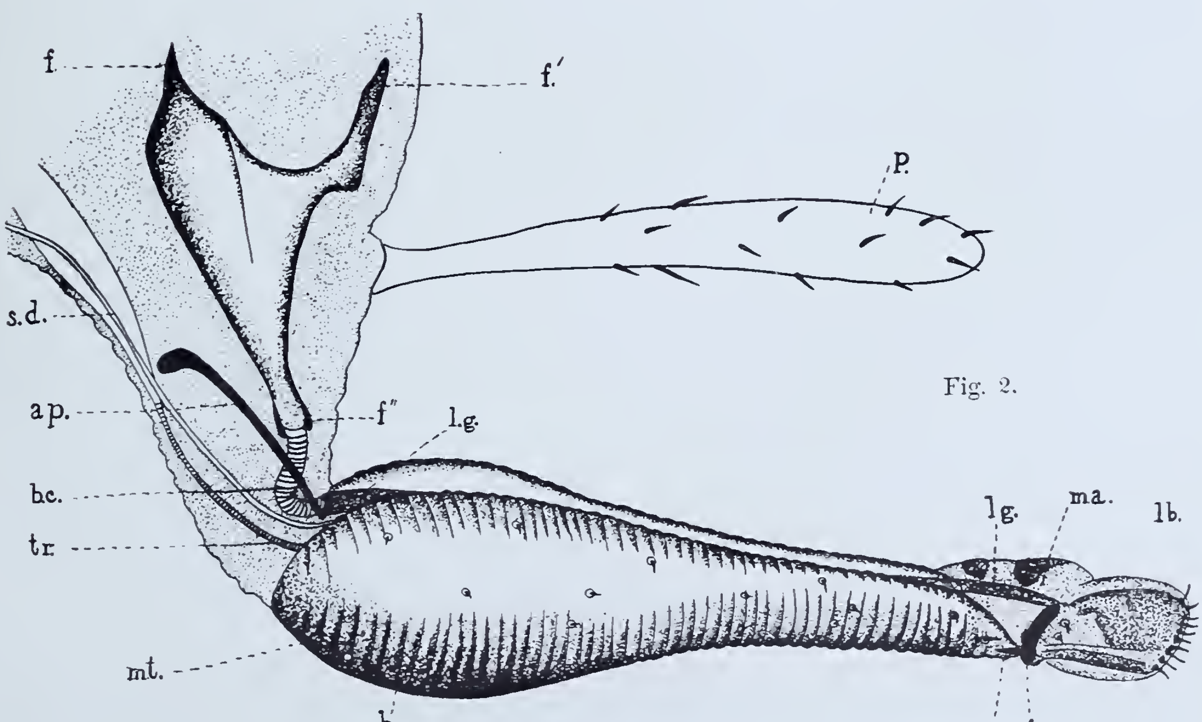

Fig. 2.

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PLATE II.

Figure 3.—The mentum and furca of *Musca nebulo.* m., mentum. i., the incision in its distal border. f., the proximal joint of the arm of the fork. f'., the distal joint, in apposition with the furca. fu., the furca. p. s., the posterior plate of thin chitin continuous with the membraneous part of the wall of the labella.

Figure 4.—The anterior wall of the haustellum of *Musca nebulo,* with the discal sclerite attached. hy., the hypopharynx partially fused with the membraneous anterior wall of the labium. m., the membrane which connects the mentum and the labial gutter. l.g., the labial gutter. l.r., the lateral rods. d.s., the discal sclerite, articulated with the lateral rods of the labial gutter.

Figure 5.—The labrum-epipharynx of *Musca nebulo.* l., labrum. ep., the epipharynx. ap., the labral apodemes.

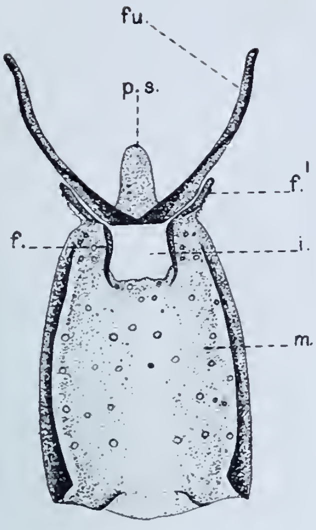
Figure 6.—Two of the prestomal teeth of *Musca pattoni,* with the terminal rings of one of the pseudotracheæ between them. t., tooth. ch. r., the chitinous filaments supporting the end of the channel. r., pseudo-tracheal ring. d.s., the discal sclerite.

Figure 7.—The prestomal teeth and terminations of the pseudotracheal channels of *Musca domestica,* after Kraepelin. t'., t''. t''' teeth of the first, second and third rows. p. s., the pseudotracheal channels. d.s., the discal sclerite.

Figure 8.—The teeth and terminations of the pseudotracheal channels of *Musca convexi frons.* t., prestomal teeth. p.s., the pseudotracheal channels. ch. r., the chitinous rods surrounding the terminations of the channels. d.s., the discal sclerite.

Figure 9.—The termination of a pseudotracheal channel in *Philæmatomyia gurnei.* p.b. the petiolated blades. p.s., the pseudotracheal channel. Note how the rings split at the proximal end; just distal to this they are much elongated. × 500.

Figure 10.—Some of the pseudotracheal rings of *Philæmatomyia gurnei* at a point distal to those of the last figure. × 500.



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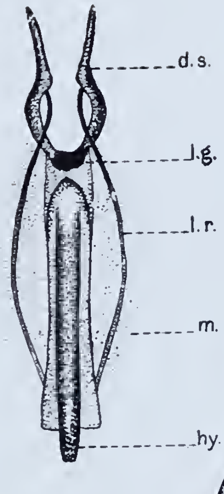

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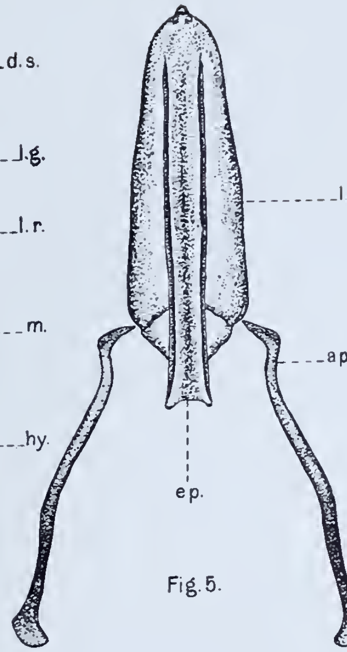

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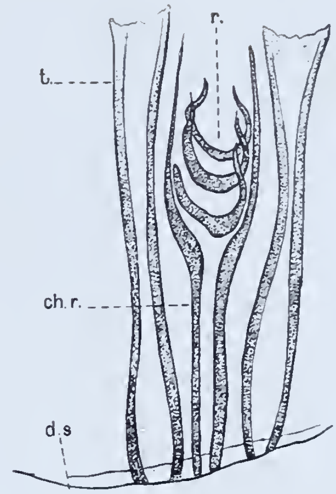

Fig.6.

Fig.10.

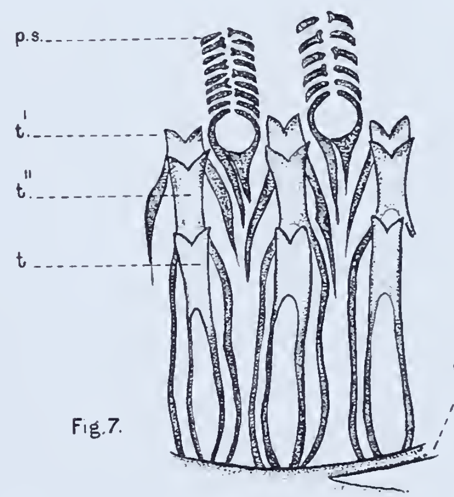

Fig.7.

Fig.9.

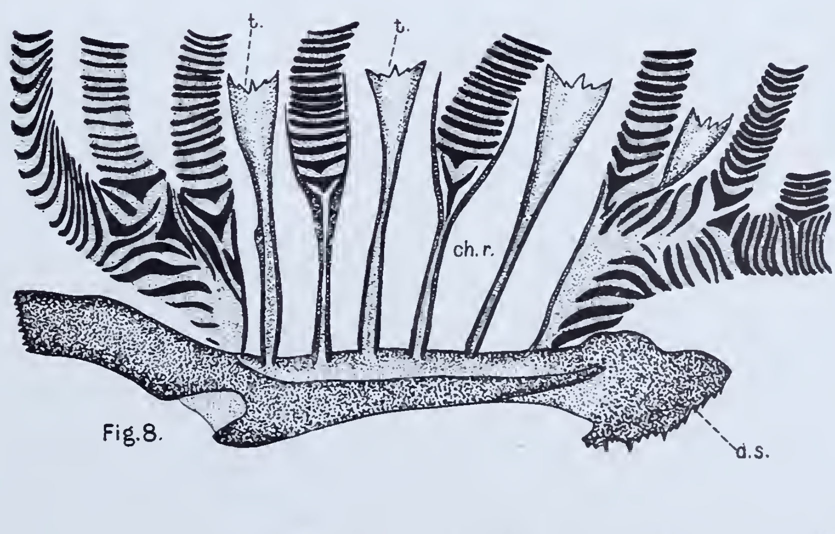

Fig.8.

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PLATE III.

Figure 11.—The proboscis of *Hæmatobia irritans*. b., the bulb. lb., the labella. ap., the labral apodeme of one side. fa., the fulcrum. b.c., the buccal cavity. p, the palps. × 80

Figure 12.—The labellum of one side, seen in profile. The position of the teeth is indicated by the dotted lines. f.l., the flaps at the distal end of the proboscis. p.s., the position of the channels on the inner wall of the flaps. p.b., the position of the petiolated blades. t., the position of the teeth. l.g., the labial gutter. fu., the furca. m.f., the proximal arm of the fork of the mentum. m.f'., the distal arm, detached and displaced forward. m., the mentum. × 180

Figure 13.—The external wall of one of the flaps, to show the shape and disposition of the squamæ, and the area over which they are deficient. × 1100.

Figure 14.—The internal wall of one of the flaps, to show the pseudotracheal channel and the sense hair at its termination. × 1100

Figure 15.—The upper end of the labial gutter, as seen in profile in a detached cleared preparation. This is the same preparation as the next figure, but as seen at a higher focus. The shaded portion represents the lateral expansion of the gutter, the dotted lines indicate the outline as seen in the next figure.

Figure 16.—As above, at the lower focus.

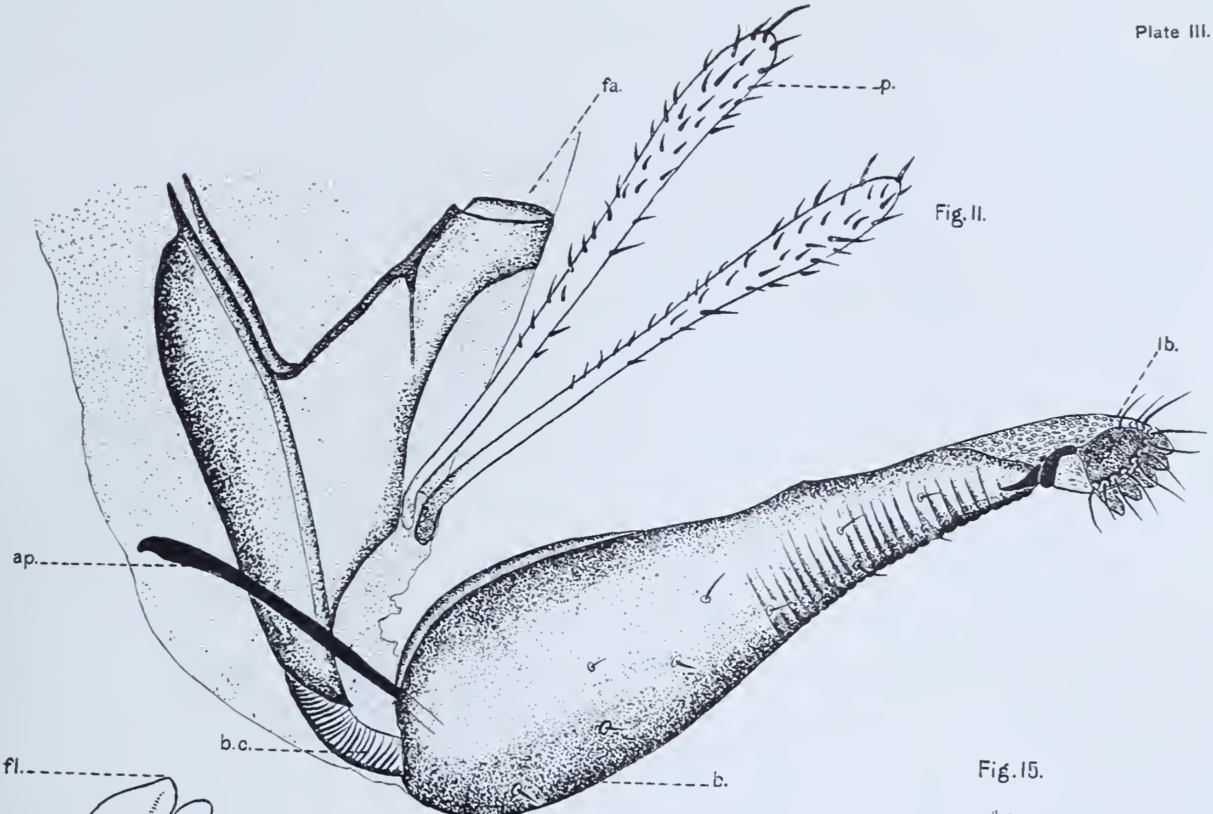
Figure 17.—The upper end of the buccal cavity, to show the method of junction with the pharynx. r., chitinous rings like those found in the salivary duct. ph., the lower end of the pharynx. × 310

Figure 18.—The first tooth in outline, to show the secondary teeth. × 700

Figure 19.—The fourth tooth. × 700

Figure 20.—One of the rod-like hairs, showing the central canal.

Figure 21.—Some of the rings of the pseudotrachea, showing the transition between the flattened plates as seen in the flaps and the typical rings as seen near the petiolated blades. × 1100



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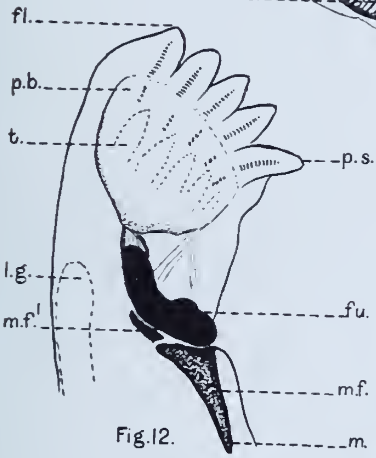

Fig. 12.

Fig. 13.

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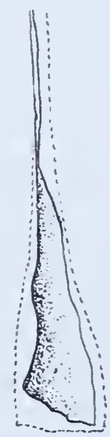

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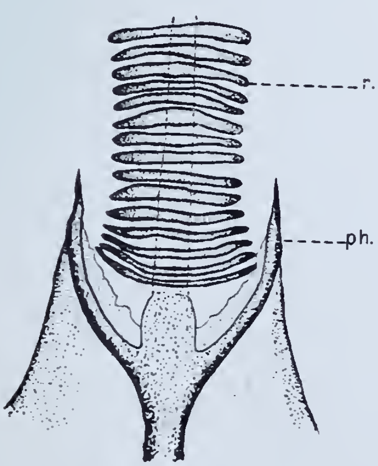

Fig. 17.

Fig. 18

Fig. 19.

Fig. 20.

Fig. 21.

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Plate IV.

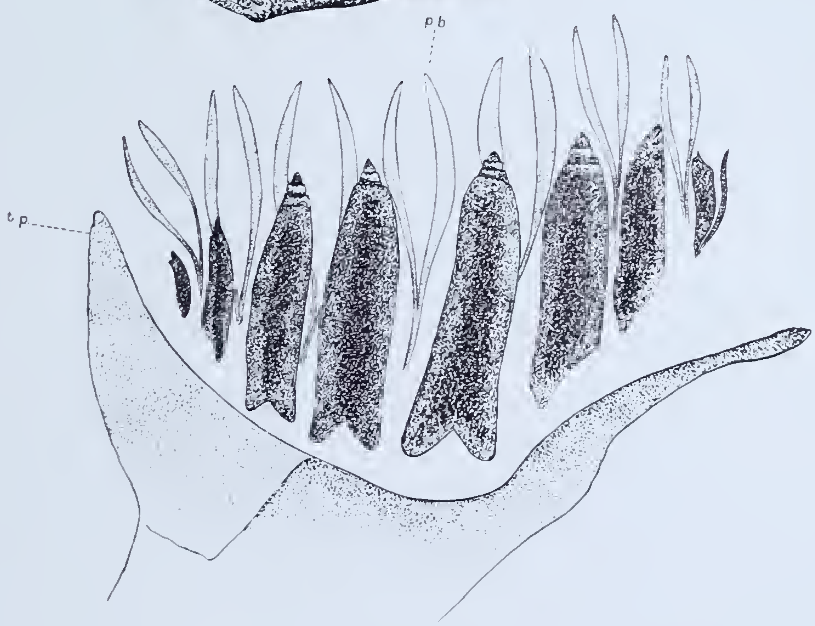
Figure 22.—The teeth and connected structures of *Hæmatobia.* The first tooth is on the left of the drawing. r.h., rod-like hairs. p.b., petiolated blades. p.s., pseudo-tracheal channels. Note the attachment of the teeth to one another at their bases. They are attached to the edge of the discal sclerite by a band of fibres, not shown. × 700

Figure 23.—The teeth and connected structures of *Philæmatomyia gurnei.* The anterior and internal angle is on the right. t.p., the tooth plate. p.b., the petiolated blades, between which lie the pseudotracheæ, as shown in Plate II, figure 9. × 475

Figure 24.—The discal sclerite and the teeth of *Philæmatomyia lineata,* seen from the side. t., the prestomal teeth. p.s., the pseudo-tracheal channels. i.a., the chitinous rods embracing the terminations of the channels, and constituting the interdental armature. r.t., the rudimentary tooth. c.c., the anterior collecting channel. c.c′., the posterior do. t.p., the tooth plate, a flange of the discal sclerite, d.s. l.r., lateral rod of the labial gutter. lb.r., labellar rod. × 600

Plate IV.

Fig. 22.



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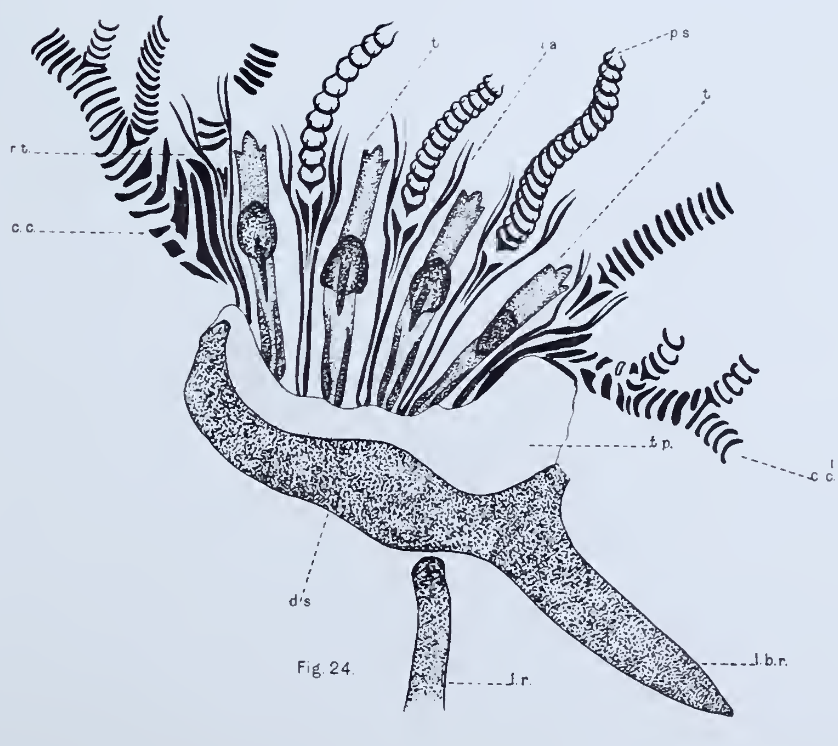


Fig. 24.

PLATE V.

Figure 25.—The discal sclerite and the distal end of the labial gutter of *Hæmatobia*. × 400

Figure 26.—The same of *Stomoxys*. × 400

Figure 27.—The discal sclerite of *Musca nebulo*, seen from the front. × 340

Figure 28.—The same, seen from the side. × 340

Figure 29.—The discal sclerite of *Philæmatomyia insignis*, seen from the side. × 130

Figure 30.—The discal sclerite of *Philæmatomyia gurnei*, flattened out and seen from the front. Camera lucida drawing. The faintly shaded area on each side of the axial apophysis is the fractured portion. × 224, *vide* page 24.

Figure 31.—The discal sclerite and the terminations of the labial gutter of *Philæmatomyia lineata*. × 300

Figure 32.—A photograph of the specimen of *Philæmatomyia gurnei* referred to in the text. I am indebted to Major Kirkpatrick, I.M.S., for this photograph. × 30

Reference letters :—ax. p., axial apophysis. lb.r., labellar rod. l.r., lateral rod of the labial gutter. m.g., the medium portion of the gutter. t.p., the tooth plate.

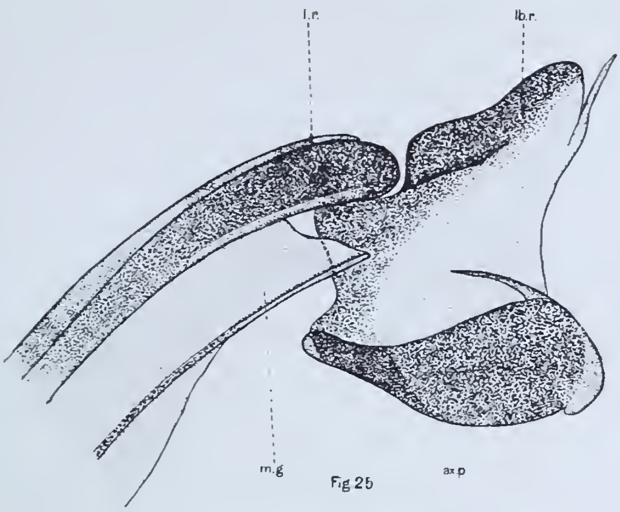


Fig 25

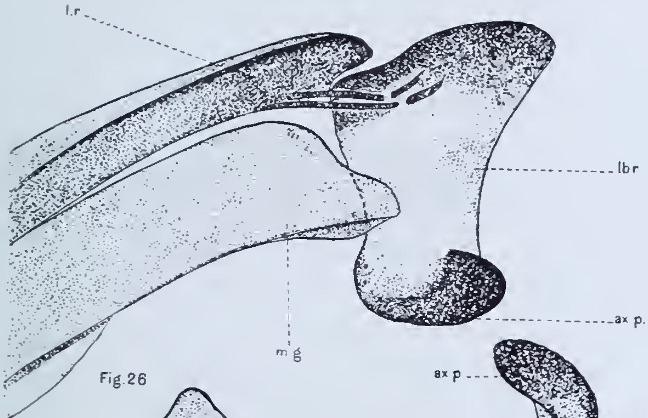
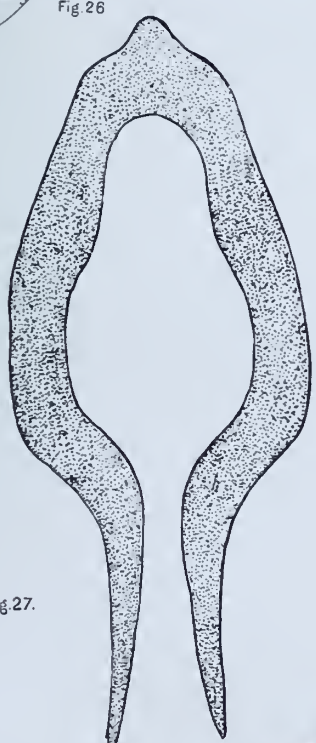


Fig.26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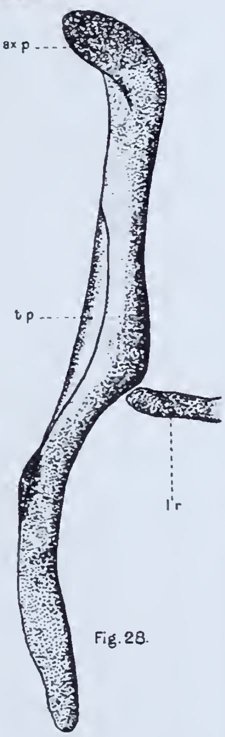

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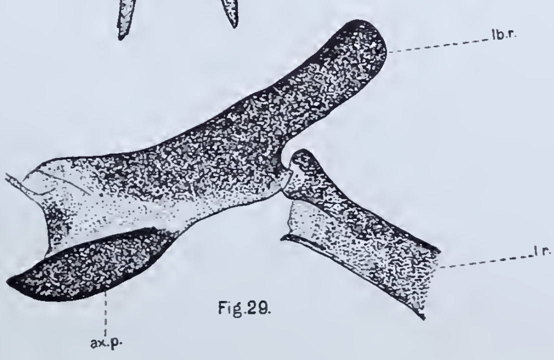

Fig.29.

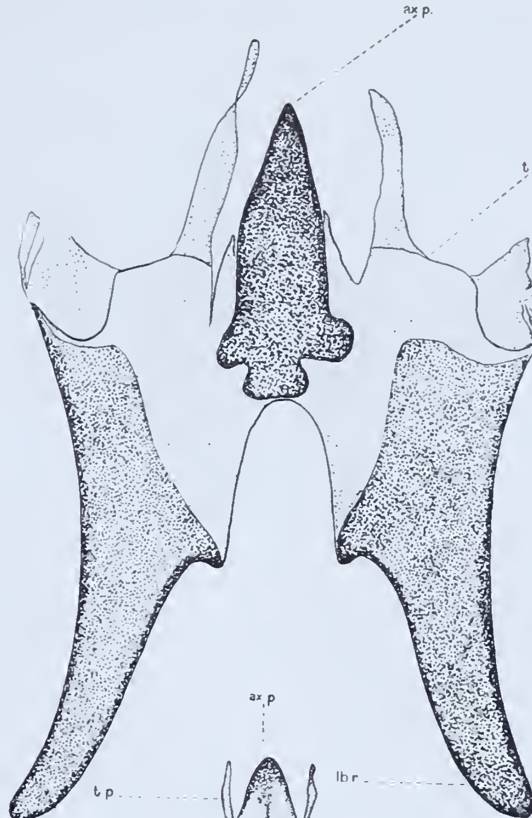

Fig.30

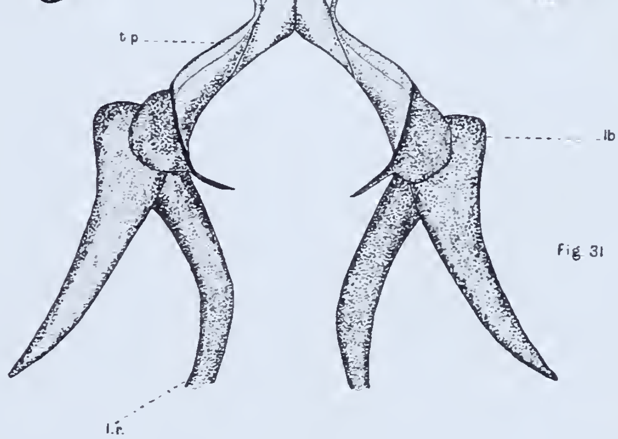

Fig 31


Fig. 32

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